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TRANSPIRATION BY CHAPARRAL AND ITS EFFECT UPON THE TEMPERATURE OF LEAVES

BY

E. B. COPELAND

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TRANSPIRATION BY CHAPARRAL AND ITS EFFECT UPON THE TEMPERATURE OF LEAVES

BY

EDWIN BINGHAM COPELAND

Three years ago, during the summer of 1928, in connection with a study of the rate of transpiration by chaparral shrubs carried on in association with the California Forest Experiment Station, I had occasion to check the temperature of leaves of some of these shrubs. The results were quite surprising, indicating possible overheating of the leaves in direct sunlight, sometimes by as much as 10° F above the shade temperature at the same time, and a lowering of usually less than this amount if transpiration was permitted. The lowering of temperature by transpiration, while understood to be a phenomenon which must result from the evaporation of water, has seldom been observed and attempts to demonstrate it have not always succeeded. Furthermore, the observed lowering has been so little as to seem to require the use of refined and very accurate methods for its measurement. The observation of comparatively great temperature differences in the case of this chaparral therefore invited verification before the results might be published with complete confidence. During the past summer, 1931, I have repeated these observations, making a large number of individual tests.

As the literature on the effect of transpiration upon temperature has been quite fully digested twice within the last decade, it will suffice here to refer to these two papers and through them to the previous work.

The first of these, by Miller and Saunders,[1] dealt with the transpiration of agricultural plants in Kansas. The authors made a very large number of reasonably consistent observations. Among their conclusions are (p. 41):

> The temperature of a leaf is influenced by the temperature of the air, by the available water supply in the soil, by air currents, by the type of leaf, by the intensity of the light to which it is exposed, and by other factors.

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[1] Miller, E. C., and Saunders, A. R., Some observations on the temperature of leaves of crop plants, Jour. Agr. Res., 26:15–43. 1923.

> Under ordinary field conditions during the daylight hours the temperature of the leaves and of the surrounding air is not constant even during so brief a period as a few seconds, but shows sudden and marked fluctuations which vary from a fraction of a degree centigrade to as much as 4° C or more.

Wherefore they dealt with averages of many and frequent determinations. From 9 A.M. to 4 P.M.:

> The average temperature of the wilted leaves of corn, sorghum, soy beans, and cowpeas was respectively 1.85°, 1.55°, 2.8°, and 4.65° C higher than the temperature of the turgid leaves.

The transpiration of turgid and wilted leaves was in ratio of 2.5/1 in corn and sorghum and 3.5/1 in cowpeas and soy beans, and to this difference in rate of transpiration is ascribed the difference in temperature.

The other paper, by Clum,[2] dealt with *Fuchsia speciosa*, *Phaseolus vulgaris*, *Brassica oleracea* (cabbage), and *Syringa vulgaris*, the work being done in New York, in the greenhouse and in the open. As he drew his conclusions, they were essentially different from those of Miller and Saunders, his summary reading:

> But in no case was a definite correlation found between the transpiration rate and the difference between the leaf and air temperatures, nor between the difference of the transpiration rates of two leaves or plants and the difference of their temperatures.

As to the validity of this conclusion, I have misgivings. A study of the experimental data seems to me to show, on the whole, that there was a relation between transpiration and leaf temperature; the temperature in most cases was lowered, and this seemed to be the result of transpiration. The results really were somewhat contradictory, however, which is the more readily understood if one notes that transpiration itself in these experiments was most erratic. For example, the transpiration rate given in his table 3 was from one-twentieth to one-half as rapid, roughly speaking, as in his table 2, both dealing with *Fuchsia* plants in pots. When one remembers that the effect of transpiration upon the temperature is, in the nature of the case, subject to interference by the use of energy in other plant functions and by the diffusion of heat from or to the plant in the course of the experiment, it is hardly to be expected that, when transpiration is exceedingly slow, it would find any uniform expression in the leaf's temperature. It is only when transpiration is decidedly active that its effects can be expected to dominate other influences to such an extent that anything like a fixed ratio between rate of transpiration and lowering of temperature is manifested.

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[2] Clum, Harold H., The effect of transpiration and environment factors on leaf temperatures. I. Transpiration, Am. Jour. Bot., 13:194, 1926.

A discussion of transpiration itself should precede a discussion of its effects. (The appropriate literature is well reviewed by Maximov.) Such a study, as I have already noted, was undertaken here three years ago. The apparent results, showing an almost unheard of rate of transpiration, provoked doubt as to their own validity. While I had complete confidence in the field observations and was therefore at first disposed to defend the conclusions, the focus of doubt shifted later to the standardization of the cobalt paper used and proved to be justified at this point. Because the statement given me as to the increment in weight of the cobalt paper used at that time in the change from blue to red was in error, the rates of transpiration which seemed to be observed had to be divided by a number between two and three. While many hundred observations were made in 1928, I have repeated only a few hundred of them in 1931. These are consistent among themselves and are consistent with those of the earlier season's work, after making the correction just indicated as necessary.

METHODS

All observations of transpiration were made with cobalt paper. The cobalt paper used this year changes color with an increment of weight amounting to between three-sixteenths and one-fourth of a milligram for each square centimeter of surface. This range, three-sixteenth to one-quarter, is the smallest within which it is safe to undertake observation of changes of color in the field. It is of course not accurate to the degree that accuracy of observation may be achieved when weighing small subjects of experiment, or measuring the volume of water absorbed, or weighing the water collected after it has been transpired. If any of the latter methods be adopted, however, the accuracy of observation is in general essentially wasted because the conditions of experiment almost always introduce other sources of error, far greater than that involved by the inaccurate recognition of color when using the cobalt paper. The use of cobalt paper has the outstanding advantages, that it permits observations so quick that the external conditions of the experiment are unlikely to change materially during the period of observation; that very many observations can be made in the time which would permit comparatively few by any other method; and, most important, that the subjects of the experiment may be under completely natural living conditions in every respect except the presence of the paper.

The general objection to the use of this method is that the presence of the blue cobalt paper in contact with the leaf subjects the leaf to an abnormal desiccating influence, and thereby is indicated a tranpiration more rapid than probably occurs in nature. This objection has a measure of validity—when it applies. If one is studying the transpiration of leaves in rather moist air, the rate apparently observed with the use of the cobalt paper is so far from the natural rate that the method is valueless unless the observations are checked with measurements by other methods, and even if so checked it remains of questionable value. On the other hand, if the application of the blue cobalt paper does not subject the leaf to a more desiccating influence than it is exposed to in nature, this objection to the method loses its force completely. Where my observations were made, it was my regular practice to dry my pieces of paper by exposing them to the sun while my observations went along. They turned back from red to blue so rapidly that three or four pieces of paper could be used over and over in a series of observations, each of which required only the fraction of a minute. The environment was so dry that it was sometimes possible to leave blue paper in the shade without its changing color, or, giving it time enough, to observe its change from red to the standard blue in the shade. Since the drying of the paper itself was accomplished under the same conditions to which the leaves were exposed in nature, it is perfectly obvious that the use of this paper so dried is not open to the objection that the transpiration observed was greater than that which took place at the same time in untested leaves.

Whether the observed transpiration was quite as rapid as was taking place in nature is another question. This may be doubted, both because the method in its nature is unable to show the effect of desiccating influences more than sufficient to turn the paper blue, and also because in the course of each test the paper changes its own desiccating power as it turns from blue to red, presumably having comparatively little power to withdraw water from the leaf when redness is approximately reached. The latter difficulty can be obviated to a considerable extent when working with subjects which transpire slowly, by using a standard of redness considerably short of the red of saturation. This is, however, not practically possible with subjects which transpire so rapidly that the period of each test, using approximately complete redness as the end, has to be measured in seconds.

One factor in transpiration, which eludes the cobalt test, is the movement of the air. The paper turns blue rapidly, sometimes within a minute, in still air in full sunshine. The cobalt test may measure transpiration under these conditions in nature. Under this condition I have never observed a lowering of the temperature of leaves in still air in sunshine to quite the temperature of the surrounding air. But with even a gentle breeze, the temperature of the leaves sometimes falls measurably below that of the air. This must result from an acceleration of transpiration beyond the rate which my method permits me to measure. As a perceptible breeze is the usual condition, the actual transpiration may be appreciably greater than my data indicate. Whether or not my data represent transpiration slower than occurs in nature, the conclusions are fairly surprising in the rate which they did show.

Everybody who has used this method to any considerable extent has probably given up the use of standard colors for constant comparison. The speed at which the observations have to be made when transpiration is active and the paper sensitive makes impracticable the use of standards for comparison of color. This work with chaparral had to be carried on so rapidly that the main problem was the perfection of a technique which would avoid gross inaccuracy in the time of starting and stopping each experiment. This technique consists in having everything needed—the piece of paper, the clips to hold it in place, the pencil, the notebook, and the leaf chosen for experiment—so located that they can be reached instantly without error, and the watch placed where the noting of the time involves no delay. In such work, with many subjects, the question is as to the number of minutes required for change of color. In this study of the chaparral it was immediately apparent that the question was one of fractions of a minute, and after the first day of preliminary work, the records were kept in seconds. With a few days' practice, the technique was so developed that I felt able to trust the notes within a margin of less than 5 seconds if the color change was rapid. It was also possible, time after time, indefinitely, to remove one piece of paper and substitute another, with a fixed interval of 10 seconds, or with an unfixed interval of usually not more than 5 seconds. To define more exactly the probable accuracy: if the period of the reaction is 30 seconds or more, the chief inaccuracy is in judgment of color and an error of 5 seconds, at the rate of judgment required is possible, but unlikely. If the period is not more than 15 seconds, rate of observation joins rate of reaction, as a factor in inaccuracy. Even so, I am sure that a 12-second record is accurate within 2 seconds, while a single 32-second record would likely be dependable within 4 seconds.

The temperature of the leaves was observed by wrapping them around the bulb of a thermometer graduated to degrees Centigrade and subject to reading with approximate accuracy to tenths of a degree. The leaf was held around the bulb with the upper, stoma-free surface exposed, the under surface being applied to the bulb. After a number of minutes the temperature became constant and was then recorded. The leaf was then turned, so that the under, stoma-bearing surface was outside and was held as before, until the temperature again became constant, when it was recorded.

The subject of most of these experiments was *Ceanothus velutinus,* which has larger leaves than any other local component of the chaparral and had already been found to be the most rapidly transpiring of such components. Using leaves as large as these, it is possible to hold them closely appressed to the bulb without having the finger and thumb in near enough proximity to the bulb to have any influence upon the record. A check of the possibility of error owing to use of the hand showed that it was possible to hold the leaf with only the nails of thumb and finger, separated from the bulb by the leaf, without visible error from this source. This was demonstrated by a series of alternate checks, using first the hand and then a paper clip to hold the leaf in place. With this particular subject, *C. velutinus,* it is possible to use a clip without damaging the leaf; but with some of the other subjects studied, this is not possible.

The study was made at Jonesville, Butte County, in the northern Sierra at an altitude of about 5000 feet. In this region chaparral is not a climax vegetation but does, as a result of fire, cover the larger part of the mountain area. This locality was chosen purely as a matter of convenience. The chaparral of this region is less decidedly xerophytic than that in any place where it is a climax formation. The resemblance to other chaparral, however, is strong enough to justify the belief that observations made here are more or less applicable throughout the State. As a mere estimate, the composition of the local chaparral is roughly: mixed manzanita species (*Arctostaphylos*), 40 per cent; *Ceanothus* species, 40 per cent; oak and chinquapin, perhaps 15 per cent; the remainder, scattered plants of service berry, cherry, *Rhamnus,* and rarely, still other plants.

I have already quoted a statement of Miller and Saunders regarding local fluctuations in temperature. We are used to accepting data on air temperatures as more exactly dependable than most of our data on plant behavior, just as physics is considered a more exact science than physiology. I can make a positive statement of a thermometer reading and it may look like a dependable datum. In fact, though, my statements as to leaf temperature are more accurate and more significant than those as to the air. Of necessity, in order to have sufficient room, I worked in open brush, on more or less stony ground exposed between clumps of chaparral. In such places, if the air is still, temperatures may differ by as much as five degrees Centigrade at points one meter apart, whether taken in sun or in shade. A reading made only 1 cm. from the leaf should therefore be satisfactory for comparison with the leaf temperature or as the temperature of the leaf's environment; my later readings were all made at this closeness to the leaf. But the air is seldom at rest; local differences cause movements even in the absence of movement on a greater scale. The effect is that the temperature at any given point commonly fluctuates appreciably within each minute. The thermometer shows almost constant change; and even so, it lags behind the changes in the air. It is because of this lag, in both the leaves and the thermometer, that statements of leaf temperature are more accurate and dependable than those of the air.

TRANSPIRATION DATA

Ceanothus velutinus (snowbrush).—During any ordinarily warm and bright sunny day, using selected leaves which stand at a right angle to the direct rays of the sun and have been so exposed for some time and thus may be supposed to be transpiring at an established rate, the period of reaction is usually 15 seconds or less—usually, in fact, less. Thus, at 10:40 A.M., August 4, with air temperature 25.2–28.1° C, reaction times with different leaves were 12, 15, 14, and 15 seconds respectively. August 14, 3:30 P.M., temperature 31°, a series of tests on one leaf showed 14, 13, 12, 12, 10 seconds. An acceleration after the first test in such series was noted many times, the first reaction sometimes being slower by one-half. At first, this made me suspect that my technique was showing a rate in excess of the natural one, but the better explanation is just the opposite: the initial slow reaction occurred while the leaf adjusted itself to a condition less desiccating than it had just been subject to.

At the beginning and close of the day the rate is slower. Thus, August 3, 5:20 P.M., temperature 28°, rate 22, 23, 22, 21 seconds; and August 13, 8:30 A.M., temperature 22°, rate 18 seconds.

The position of the leaf is critically important. Thus, in four successive tests showing rates of 15, 17, 20, and 15 seconds, it could be seen that the first and last were on leaves more exactly transverse to the light than the other two. The leaves of this plant are seldom flat, but are more nearly so in early than in late summer. The change effects a real economy of water, which becomes scant with the passing of the season, for only a minor part of the very wavy leaves is exposed to the full light of August. Three pairs of tests, each pair on different parts of a single leaf in its natural position, showed, in seconds:

Transverse to sun	18	15	17
Oblique to sun	25	24	24

All the foregoing tests were made on the under surface, the 1928 work having showed that the loss of water from the upper surface is less than the likely error in tests of loss of water from the under one. The reaction in 1928 probably showed the loss of about 0.3 mg. per cm.^{2} of surface (the datum supplied me with the cobalt paper was 0.665 mg.). A few of the 1928 data will be used, where relative transpiration is all that it is intended to show in order to illustrate facts which it seemed unnecessary to demonstrate again in 1931. In order to determine what differences in rate of transpiration may be correlated with the aging of the leaves, the leaves on one twig, numbered from the youngest to the oldest, were tested with the following results:

	ALL IN SUN	UNDER SURFACE	UPPER SURFACE
1	¼ grown	35 seconds	2 minutes
2	½ grown	30 seconds	10 minutes
3	grown	35 seconds	17 minutes
4	grown	25 seconds	25 minutes
5	grown	30 seconds	30+ minutes
6	grown	30 seconds	30+ minutes

Merely to show that the season of active transpiration extends through the whole of the local summer season, the following data are presented:

July 11, 4:00 P.M., temperature 87° F in sun.
  In sun, 20, 20, 20, 25, 20 seconds.
  Shade, 30, 30 seconds.

July 18, 3:30 P.M., 85° F in sun.
  In sun, 20, 20 seconds.
  Light shade, 30 seconds.
  Deep shade, 90 seconds.

July 21, 4:30 P.M., 90° F in sun.
In sun, 15, 12 seconds.
August 16, 3:30 P.M., 89° F in sun.
In sun, 20, 15, 20, 15, 12, 15, 12, 12 seconds.
August 18, 4:45 P.M., 81.5° F in sun.
Under hilltip, in sun, 35, 40, 30 seconds.
[8] September 22, 3:30 P.M., 78.5° F (smoky).
In sun, 25, 25 seconds.
Shade, 25, 45, 40 seconds.

In order to test the ability of snowbrush to regulate its transpiration, a leaf was removed from its stem and placed in the sun and the following record made of the time required for change of color of paper:

August 16, 4:15 P.M.—15, 15, 12, 15, 15, 15, 15, 20, 15, 20, 25, 20, 20, 15, 20, 20, 15, 15, 15, 15, 25, 20, 20, 20, 20, 25, 35, 55, 64,— leaf stiffening, dry.

At the end of this series of experiments the leaf was becoming stiff with dryness. There seemed to be a very moderate checking of transpiration almost immediately after the separation of the leaf from the stem (compare the data of same date in preceding table), but it is evident that *C. velutinus,* so long as it is exposed to the sun, has only a very limited power to economize its water by checking its transpiration. This explains the distribution of snowbrush. It occurs on slopes and in pockets, where water from higher ground may reach it, but it is not found on the drier slopes and hilltops. The plants tested August 18 are at the extreme limit of its local occurrence. The top of this hill is too dry for snowbush but is suitable for manzanita and dwarf oak.

A considerable number of tests of transpiration in the shade have usually required two or three times as long as those in the sun, sometimes much longer. These are not reported, because all that they really show is the density of the shade, and this of course may range from the brightest diffuse light to complete darkness. One shade reaction took place in 20 seconds and its validity is mistrusted because it occurred on an exceptional day when the light was weak and the air damp—that is, under such conditions that the cobalt test is likely to extract an unnatural amount of water.

Ceanothus cordulatus (buck-brush).—In the immediate locality where most of these tests were made, this is the commonest single

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[8] The air on September 22 was so smoky that the attempt to carry the season's observations through another month was rather a failure. This was the first afternoon during this study when an effort was needed to secure blue paper. On this day it had to be placed on stones fully exposed to the sun, to get it as fully blue as on preceding days.

Ceanothus species. Because of the smallness of the leaves and the weakness of their petioles, it is a particularly inconvenient subject for this kind of experiment. In its rate of transpiration it is apparently not different from *C. velutinus*, the tests made having identically the same range. Representative 1931 data are:

August 14, 3:40 P.M., temperature 28° C; successive tests on one leaf, 20, 13, 13, 13, 13 seconds.

August 5, 5:05 P.M., temperature 31° C; successive tests 26, 22, 20, 21, 18 seconds.

The 1928 tests ran steadily between 20 and 25 seconds. A leaf plucked and tested, as has already been reported for *C. velutinus*, gave the following results: 20, 20, 20, 20, 15, 20, 15, 20, 20, 20, 20, 20, 20, 20, 25, 25, 20, 35 (drying), 25, 35, 85, 100 seconds. As in the other species, there is but little checking in the rate of transpiration until the water in the leaf is exhausted to the point where the leaf begins to become brittle. This requires a shorter time for *C. cordulatus* because the leaf is thinner.

Ceanothus prostratus, locally known as squaw carpet or mahala mat, is not chaparral but a ground cover in open woods. It was tested on only one day and the transpiration seems to be appreciably slower than that of the other species of its genus, requiring about 40 seconds for the change of color.

Arctostaphylos patula.—This is H. F. Copeland's identification of the plants tested. Other species are also present in the chaparral. The leaves are quite uniformly set edgewise on some bushes, on others they vary, and only rarely are they in large part crosswise, in the ordinary leaf position. The transpiration by manzanita is somewhat slower than that of snowbush and buck-brush. That of the under surface is materially slower, but this is partly compensated by the fact that the morphological upper surface is also active in transpiration. These plants were tested throughout the season, but it will suffice to give the following excerpts from the data obtained June 22: under surface, 50, 70, 50, 60, 55 seconds; upper surface, 90, 60, 60, 90, 65 seconds. The few 1931 tests showed somewhat more rapid transpiration—about 30 seconds from the under surface and 35 seconds from the upper, for each test. These were made on leaves transverse to the light rays; and as this is not the position most common in nature, they represent unnatural speed. Unlike *Ceanothus,* manzanita shades the ground very incompletely. With manzanita, in contrast to the *Ceanothus* species, there seemed to be a slowing down of the transpiration rate in the afternoon of hot days, and this was probably particularly the case with bushes whose leaves stood uniformly edgewise. The number of observations substantiating this conclusion, however, was too small to make it positive.

Of the less common chaparral components, *Rhamnus californica* transpires as rapidly as manzanita but less rapidly than snowbush.

The service berry (*Amelanchier*) is almost as active as *Ceanothus,* the color change occurring frequently in as short a time as 20 seconds.

Castanopsis sempervirens (chinquapin).—For reasons which have nothing to do with transpiration, the oaks have been regarded in southern California as the most desirable constituents of the chaparral for our purpose. Because of this preference, it seemed desirable to pay particular attention to them in this study. The commonest member of the oak family in this region is the dwarf chinquapin. Tests of the influence of leaf age give results for the under surface running up to 3 minutes in the case of very young leaves and accelerating as they approach maturity; up to 3.5 and 4 minutes for the upper surface of half-grown leaves, the time increasing to 8 or 10 minutes as they reach full size, and still longer intervals thereafter. As the immature leaves, which alone transpire from the upper surface actively enough to merit attention, are altogether a minor element in the vegetation, the upper surface in this case (as in that of all subjects except manzanita) was dropped from further consideration.

Records from the mature leaves in full sunlight, made June 20, follow: 20, 30, 40, 45, 45, 40, 40, 40, 40, 30, 30, 30, 30, 30, 30, 30, 30, 30, 35, 35, 35, 35 seconds.

At the same time, fourteen tests made in the partial shade of the interior of the brush ran from 45 to 90 seconds.

July 14, 12 M.
    In sun: 40, 30, 25, 20, 25, 30, 35, 25, 30 seconds.
    Shade: 40, 50 (and with edge to sun) 40 seconds.
July 18, 3:00 P.M., 89°; 50, 55, 50, 45 seconds.
August 19, 4:00 P.M., 91°; 30, 40, 35 seconds.
September 22, 4:00 P.M., 76°; 30, 30, 30, 30 seconds.

Influenced particularly by these rapid reactions of September 22, 1928, I hesitated to estimate the transpiration of *Castanopsis* at less than two-thirds that of *Ceanothus.* On the basis, however, of tests made in 1931 for the purpose of this comparison, I regard less than one-half as a better justified ratio. The data already given for:

C. velutinus, 14, 13, 12, 12, 10 seconds.
C. cordulatus, 20, 13, 13, 13, 13 seconds.

were taken within the same ten minutes as

Cast. sempervirens, 42, 38, 42, 43 seconds.

These tests were late in the day for maximum transpiration by *Castanopsis;* but even noon observations in 1931 never showed a reaction time of less than 30 seconds.

A checking of transpiration with want or loss of water, which is in the case of *Ceanothus* notable for the doubtful or moderate extent to which it can be observed, is very evident in *Castanopsis.* This probably explains the contrasting data for July 18 and the other figures presented. July 14 and 18 were the brightest and windiest days on which any of these tests were made and a water deficit in the plant, effective in late afternoon, was almost surely responsible for the slow transpiration on July 18. This automatic control of transpiration finds a ready expression in the behavior of the plucked leaves; after the unreplaced loss of only enough water to change the color twice, the transpiration is greatly reduced. The following series of readings, with 10-second intervals between, in plucked leaves, illustrates this:

July 16: 35, 35, 140, 145 seconds.
July 14: 30, 35, 90, 80, 90, 85, 110, 90, 90 seconds.
August 16: 25, 35, 65, 85, 80 seconds.

Castanopsis may transpire half as rapidly as *Ceanothus* when both are supplied with all the water they can use, but with any decrease in the water supply, the difference immediately becomes much greater. It is therefore able to thrive in places too dry for the local species of *Ceanothus.*

Quercus vaccinifolia.—This dwarf oak is common in the northern Sierra chaparral, particularly on dry slopes. The nearest flat hilltop, too dry for any *Ceanothus velutinus,* is occupied largely by manzanita with a considerable intermixture of dwarf oak. Tests made here on June 23, 1928, showed transpiration from the under leaf surface sufficient to effect the color change in 45 or 50 seconds. On August 18, temperature 83° F, tests gave consistent counts of 55 seconds. Tests in 1931, on a clump adjacent to the most tested clumps of *Ceanothus,* with the somewhat more rapid paper, still showed a reaction time of seldom less than 55 seconds.

Quercus Kelloggii (Black oak).—While this oak is not typically a chaparral plant, as the term is usually understood, for the reason that, given time, it will become a tree, it nevertheless behaves in many respects like chaparral and has the advantages of the chaparral of high elevation in its ability to grow without a nurse crop and to recover from fire by putting out suckers. In its transpiration it is no more active than the chinquapin. It happens that my records on it were made under conditions particularly favorable for rapid transpiration, but its comparative inactivity is illustrated by records made on *Ceanothus velutinus* at the same time.

June 23.
    Q. Kelloggii, 45, 30, 35, 40 seconds.
    C. velutinus, 25, 15, 20, 15 seconds.
July 21, 87°.
    Q. Kelloggii, 40, 25, 35, 25, 25 seconds.
    C. velutinus, 15, 12 seconds.
August 18.
    Q. Kelloggii, 120, 100 seconds.
    C. velutinus, 35, 40, 30 seconds.

Under conditions favorable to the most rapid transpiration, the loss of water from the oak is not more than half as rapid as that from snowbrush. With scarcity of water, the difference would be greater.[4]

TRANSPIRATION: ARGUMENT

The test of paper used in 1931 showed an increment in weight of three-sixteenths to one-fourth mgs. per square cm. Let us use one-fourth, to keep round numbers. If this change was accomplished in 15 seconds, that much water was given off by the leaf and absorbed by the paper. This is very little water, but the time likewise is very short and the indicated transpiration is exceedingly active. Such a rate was usually to be observed with *Ceanothus valutinus* in direct sunlight as early in the day as 9:00 A.M.; and as late as 5:00 P.M., and not rarely as late as 6:00 in the afternoon. Sunshine in these mountains is practically uninterrupted during the summer. If the indicated rate of transpiration is maintained for a 10-hour day, the loss of water amounts to 0.60 grams, and if this rate is maintained for 100 days it amounts to 60 grams—a column of water two feet in depth. While the maximum transpiration lasts only about 8 hours, it goes on more slowly for several additional hours; in all, reasonably the equivalent of 10 hours at the maximum rate, for a summer of not less than 100 days—the whole of June, July, and August, and a large part at least of September—and the rate of transpiration in the case of both common *Ceanothus* species in full sunshine is more rapid than will produce the color change in 15 seconds.

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[4] *Quercus Kelloggii* has a wider range in altitude and in other respects, than any other local tree. The statements just made may not apply to it elsewhere than in chaparral.

If the interest in these figures were confined to the field of plant physiology, the inaccuracies involved in the preceding calculations, as well as in the experiments themselves, would be serious, and the probable error in reporting less transpiration than occurs in nature would be just as serious as if it occurred in the other direction. The data and calculations presented have, however, an interest beyond the field of strict botany, in that they can be used to provide an idea of the rate at which the chaparral removes water from the soil and thus from eventual industrial use of any kind. Looked at in this manner, the matter of interest is not primarily the rate of transpiration per unit of leaf area, but the rate of removal of water per unit of land area. Such applications of the observed rates of transpiration are sometimes made laboriously and with more semblance than reality of dependability, by counting leaves and measuring their area. The fact in this case, and practically always in nature, is that the total leaf area exceeds the ground area, sometimes many times. The maximum area exposed to full sunlight by the foliage cannot be greater than the total of the ground area. How nearly it approximates the ground area might be determined by measuring the part of the ground area to which direct sunlight penetrates through the foliage. In well developed chaparral, this ground area upon which the sun directly shines at any particular time of the day is an insignificant fraction of the total area. Just what it is would have to be determined a great number of times before a ratio applicable to chaparral in general could be established.

Besides the leaves which are in direct sunlight and which transpire at the rate represented by most of the figures which have here been presented, there is at all times a great area of foliage in the shade of the directly illuminated leaves. These lightly or densely shaded leaves likewise transpire at a rate, which in my tests usually varied between one-third and one-half that of the fully illuminated leaves. The area of foliage in this light or dense shade is several times the area of the ground which receives direct sunlight.

If we assume therefore that the area of foliage transpiring as under the influence of direct sunlight is equal to the area of the land covered by the chaparral, the error introduced will again be on the side of showing less water transpired than actually, in nature, does go into the air through the plant from the soil.

In other words, if we conclude from the fact that two feet of water is transpired from each given area of foliage that two feet of water is taken from each unit of land area during the same season, we shall quite certainly show less loss of water than actually occurs.

Of course the chaparral does not transpire more water than is available. It may transpire all that it can get; to a great extent it must do this, else the composition of the chaparral would not be determined, spot by spot, by the water supply, and it is plain that it is so determined. The average annual precipitation at Jonesville is nearly or quite 50 inches. Drainage is by Butte Creek. There are dependable records of the run-off by Butte Creek, but there is no interest in a check of these against the precipitation, because a large part of the catchment area is drier country. It is my belief that evaporation directly from the soil is negligible, perhaps not exceeding the local loss through the soil (recoverable from wells in the valley). Approximately, the summer stream flow is the balance of the water which has entered the ground, after the plants have absorbed and transpired what they are able to get and handle.

Our mountains and their vegetation are of economic value in a number of ways, but their service as sources of water completely overshadows their value in all other respects. In southern California this importance of water is fully appreciated, and with increase of population and intensification of agriculture, conditions in northern California will presently be different only because the total water supply is greater in the North. The loss of two feet of water, in the south and in the north, is entitled to respect and demands a new kind of study of the vegetation as a whole. If transpiration at anything like this rate is occurring from the chaparral in any place where chaparral is the climax vegetation, the resulting loss of water from the land is so serious that no other aspect of the art of forestry is of nearly equal importance to possible reduction of this transpiration.

There have been very many scattered observations which should have prepared us to expect some such figures as these. Aside from the studies already referred to (summarized by Maximov), which have shown that sclerophyllous vegetation is active in transpiration, it has been observed repeatedly that one effect of removal of the chaparral is a prompt increase in the amount of water in the soil. The Forest Service is in possession of numerous reports of the occurrence of springs and patches of moist ground where water was not previously indicated, after the burning off of the chaparral has prevented its natural loss by transpiration. Figures not reported here show that neither willow nor alder transpires as vigorously as do the components of the chaparral, but it is common information in the mountains that a small stream running from a thicket of willow or alder can be made to produce more water by the removal of these plants.

While the water transpired by the chaparral would in large part augment the stream flow if it were not transpired, we must not conclude that the removal of the chaparral would make our hill and mountain areas more productive sources of water for irrigation or other use. This is not the place for a detailed argument on the necessity for a cover of vegetation, either for the conservation of water or as a nurse for a subsequent forest. The simple fact is that we must have some kind of vegetative cover because in its absence the soil would presently be removed from our mountains, and their stony skeletons would permit the water falling there to run away on the surface; and, instead of an increase in spring water through the removal of the chaparral, the final result would be a succession of arid, stony hills and mountains with hardly any springs at all.

The practically important conclusion from these tests, aside from their demanding attention to the fact that transpiration involves a very great loss of water, is the demonstration that the consituents of the chaparral are quite unlike in this respect. If our *Ceanothus* were entirely replaced by dwarf oak and black oak, the transpiration would be cut in half. At the worst, the productivity of the soil and its water-retaining power would certainly not be hurt by such a change in the vegetation. The data herein presented show clearly that such a modification of the chaparral would very greatly increase our water resources, and invite a study of the possibility of effecting a change in this direction. While the oaks are the components of our local chaparral most economical of water, it may well be that there are other hardy brushy plants, able to thrive in the same areas, which would be still more economical. The propriety of a study of this kind and of a study covering the chaparral constituents of the parts of California where the water problem is already critical, is too clear to need to be more than suggested.

Observations too incomplete to be ready for publication indicate that the chaparral is more wasteful of water than either of the other general types of vegetation usually considered as possible substitutes—grass and evergreen forest. The effort of the Forest Service at all times is to effect a return to coniferous forest, and the chaparral is prized for the double reason that it restricts erosion and serves as a nurse crop for the coniferous vegetation unable to secure a place without such a nurse. My limited observations indicate that yellow pine, the commonest lumber tree of this region, is decidedly more moderate in its demand for water than are even the oaks.

LEAF TEMPERATURE

It is easy in direct sunshine, at any time during the summer season, to observe a raising of the temperature amounting to several degrees, in leaves wrapped around the bulb of a thermometer with the upper surface outside, and a lowering of less or more than the same number of degrees when the leaf is reversed. The actually observed differences, with leaves which transpire actively, range commonly between 4° and 10° C. I was for some time unable to account for the wide range of observed differences but found finally that they result primarily from variations in the respective positions of the leaf and thermometer. To get maximum results it is even more essential in this work than in the tests of transpiration that the subject be placed in the plane exactly at right angles to the incident rays. Any error in this position, even such as occurs from minor carelessness, has a very evident effect on the result. I was slow to recognize the importance of exactness in the position of the thermometer and the leaf, for the following reason: even if the thermometer is in the plane perpendicular to the rays, only a narrow strip of the leaf receives the rays at a right angle. A far larger area of the leaf is obviously illuminated at an oblique angle; and under the thermometer it is shaded. It was not easy to believe that exactness in the position of a narrow strip of leaf could have a marked effect on the reading of the thermometer, half of the bulb of which was in contact with shaded leaf, and most of the remainder in contact with obliquely illuminated leaf. With my technique, it was impossible to test the extent to which flatly expanded and properly placed leaves might overheat if kept from transpiring.

The critical importance of the position of the subject being clearly established, all readings considerably less than the maximum observed under similar outside conditions could be regarded as owing to faulty manipulation, and they were discarded. Interest attaches accordingly, only to the greatest observed differences and these only will be reported. These could be found in substantially the same amount at any time during the day from 10 A.M. to 4 P.M., and without much decrease for an hour or two longer in each direction. Any cloudiness or haziness, or the smoke from a distant fire, decreases in marked degree both the transpiration and the temperature reaction.

In the case of *Ceanothus velutinus,* on bright days I have repeatedly observed an increment, above the temperature of the air, of more than 8° C in a leaf applied to the bulb, with the upper surface exposed to the sun. The rise takes place at a rate of about 1° per minute; somewhat faster at first and more slowly as the maximum is approached. I have observed several times an increment of as much as 10°. The maximum observed was on August 12 at 4:00 P.M., with a fluctuating shade temperature of 20° to 22°. The temperature of the leaf rose to 32°. It was then reversed, with the under surface outside, and the temperature dropped to 21°, still in the sun. The drop is more rapid than the rise, requiring usually about one-half as many minutes. The leaf was then shaded by interposition of a handkerchief between it and the sun. The temperature dropped to 18.6°. With the removal of the handkerchief it rose to only 20°; the leaf being reversed again, with the upper surface outside, the temperature rose once more to 32°.

As the transpiration might well not be the only factor responsible for the lowering of the temperature of the leaf when it is reversed, repeated observations were made, in which after the leaf was tested with the upper and then with the under surface exposed, the under surface was covered with a thin layer of liquid vaseline. An observation taken August 2 at 10:15 A.M. will illustrate the results. The shade temperature was 32.8°; with the upper surface exposed the temperature rose to 40°; with the under surface exposed it fell to 33.6°; with the under surface vaselined it rose to 41°. Similarly on August 3, at the same hour: shade temperature 27°; with the upper surface exposed, 37°; under surface exposed, 29°; vaselined, 37.3°. On the same day at 2:00 P.M., series of leaf tests simultaneously showed:

Upper surface exposed	Under surface exposed	Under surface vaselined
39.5°	29.5°	38.5°
38.5°	33.5°	41°
39°	29.5°	40.5°

In the first of the experiments reported the leaf was held at all times with a clip. In the others it was held with the fingers, but it will be noted that if the temperature of the fingers had any effect it must have been to decrease the differences observed, because the higher ones are above and the lower ones are below the blood temperature.

The other constituent of the chaparral, which rivals *C. velutinus* in rapidity of transpiration, is *C. cordulatus.* Its leaves are too small for convenient use by the technique employed and the observed temperature differences ran only from 4° to 7.2°.

Quercus vaccinifolia transpires in general about one-half as rapidly as the two *Ceanothus* species. With a shade temperature of 31.2°, the temperature of a leaf with the upper surface exposed rose to 39° and with the under surface exposed dropped to 35°. The lowering is about one-half as much as was observed at the same time with *C. cuneatus* (7.2°), and did not suffice to bring the temperature of the leaf down nearly to that of the shade at the same time.

Castanopsis sempervirens transpires at about the same rate as *Quercus* and shows even less temperature differences. With the shade temperature 33°, leaf temperature with the upper surface exposed, rose to 38.9° and dropped only to about 37° when the leaf was reversed. With the application of vaseline, the temperature rose to 39°. A leaf of *Amelanchier,* an uncommon chaparral constituent tested several times, constantly showed a temperature with the upper surface exposed of 33° and would drop only to 31.6° when the leaf was reversed, the shade temperature being about 1° lower still. This subject is intermediate between the oaks and the *Ceanothus* in rate of transpiration and the comparatively slight difference in observed temperatures is not explained. It may be owing to the thinness of the leaves and correspondingly rapid radiation, preventing the accumulation of much heat when transpiration is prevented. Leaves of *Spiraea,* not properly a chaparral constituent because it usually grows on moister ground than lends itself to the development of chaparral, showed temperatures with the upper surface exposed of 31°; with the under surface exposed of 27°; and an air temperature fractionally below 27°. In spite of the considerable differences in temperature, the transpiration of this subject is not much more rapid than that of the oaks. It also has comparatively thin leaves.

Arctostaphylos patula, which with the two *Ceanothus* species makes up the great bulk of the chaparral, has stomata on both surfaces and the leaves tend to be so placed that the edges are toward the sky and the ground. The morphologically under surface transpires slightly more rapidly than the morphologically upper surface, the differences commonly being from 10 to 15 or 20 per cent. Several tests showed a difference of about 1° in temperature, according to which surface was placed outside when these leaves were wrapped around the thermometer bulb.

Salix scouleriana, a willow remarkable for its occasional appearance in chaparral areas, showed a leaf temperature with the upper surface exposed of 32° and with the under surface exposed of 28.4° in still air, but a further drop to 28° with the advent of a breeze.

The phenomena of cooling, which have been reported are ascribed to transpiration as a cause:

1. On the ground of antecedent reasonableness. Rapid evaporation inevitably has such an effect.
2. Because, comparing subjects, the plants which transpire most rapidly show the greatest cooling.
3. Because, considering the one most studied subject, *Ceanothus velutinus*, the transpiration and the cooling are influenced alike, by (*a*) the strength of the illumination and (*b*) the angle of illumination.
4. Because, if transpiration be prevented by coating the under surface with vaseline, the illumination of the under surface results in essentially the same overheating as the illumination of the upper surface.

SUMMARY

1. Where these studies were made, in the northern Sierra Nevada at an altitude of one mile, the most actively transpiring common components of the chaparral, *Ceanothus velutinus* and *C. cordulatus,* give off water at a rate representing a loss of two feet of water per unit of leaf area during the active season. In this locality they took from the soil and transpired this amount of water.

2. This may reasonably be interpreted as representing a loss of two feet or more of water per unit of ground area. Since the primary function of chaparral, in human economics, is the conservation of soil moisture, these shrubs must be regarded as very uneconomic.

3. Other constituents of the chaparral transpire more slowly; *Quercus vaccinifolia* and *Castanopsis sempervirens* not more than half as fast. Replacement of *Ceanothus* by these species would result in the saving of a foot of soil water. Replacement of chaparral by pine forest would probably effect a still greater economy.

4. Transpiration restrains the heating of the leaves by insolation, the observed cooling of very actively transpiring leaves amounting sometimes to more than 10° Centigrade. More appropriate technique might reveal a considerably greater cooling effect. In a breeze, leaves transpiring in the sun are sometimes cooled below the shade temperature of the air.

BRAZILIAN FERNS COLLECTED BY YNES MEXIA

BY

E. B. COPELAND

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BRAZILIAN FERNS COLLECTED BY YNES MEXIA

BY

EDWIN BINGHAM COPELAND

Mrs. Ynes Mexia, previously well known for her excellent collections of Mexican plants, has been collecting in South America during the past two years, spending about 22 months in Brazil. One year of this was devoted to the neighborhood of the Agricultural Experiment Station at Viçosa, Minas Geraes. In this way she probably made more complete collections there than have ever been made for any one locality in the interior of Brazil. On short-time trips she visited the mountains near Rio de Janeiro, about Diamantina, and elsewhere in Minas, and near Belem in Pará. She then ascended the Amazon and is now in Peru. Her total collections of Pteridophytes are nearly 300 numbers. Apparently eight of these represent new species. This small proportion is added evidence of the well-known fact that the state of Minas Geraes has been fully collected in the past. This is especially evident when it is further noted that four of the novelties are tree ferns. It seems to be equally the case here and in the Orient, that *Cyathea* develops peculiar forms in each locality and that the collection of really complete specimens is necessary for their recognition. Mrs. Mexia's study set is of such specimens as we rarely see from the tropics, including in every case a practically complete representation of the features of the plant. Cyatheas may be sufficiently alike to pass as one species if all that is collected is the usual fragment consisting of a pinna and a piece of the rachis; but may be very evidently distinct when only the stipe and a chip from the trunk are collected. The identity of characters of the fragments may be so complete that even when we know we have more than one species to deal with it remains impossible to assign the fragments with certainty. This being so, the identity of some of the earlier described species may never be established positively.

I have been fortunate enough to have the assistance of Dr. Carl Christensen in the identification of Dryopteris, and take pleasure in including with my own notes his description of one species and his note on another.

The types are all in the Herbarium of the University of California.

Cyathea armata (Sw.) Copel. comb. nov.

Polypodium armatum Sw., Prod. Veg. Ind. Occ. (1788), p. 134.

It has been general usage to include under this name a group of distinguishable entities spread well over the American tropics. Maxon, Contr. U. S. Nat. Herb., 24 (1922), 33 et seq., has undertaken the discrimination of the North American forms, and regards this species in a strict sense as known only from Jamaica and Cuba. As to South American species, he states: "It has a close relative also in the Brazilian *A. hirta* Kaulf., which together with the other South American species of this group, is in need of critical revision." It certainly is, leaving what I accept as *Alsophila hirta* out of account. Our herbarium contains not less than five species grouped under *C. armata.* It is convenient for the moment, calling attention to this condition, to leave it unremedied, and construe *C. armata* in its usual very broad sense. Mrs. Mexia has then collected it twice, Nos. 4239, with weakly muricate stipes clothed at the base with lanceolate to linear chestnut paleae with pale margins; and 4956, with spiny stipe and broader gray paleae.

Cyathea setosa (Kaulfuss) Copel. comb. nov.

Alsophila setosa Kaulfuss, Enum., p. 249.

Changing the generic name of a long-known plant is usually anything but a source of pleasure, but in this instance I do it with real satisfaction—its nomenclatorial history illustrates so perfectly the fatuity of the attempt to maintain *Alsophila* and *Hemitelia* as genera defined by indusial characters alone. Its original description, under *Alsophila,* says: "Sori globosi, indusio tenuissimo laceratim reclinante tecti." Kaulfuss adds: "Auctor huius generis, *Rob. Brownius,* summam cum Cyathea adfinitatem agnoscit, nec mihi certas eruere inter hanc et Alsophilam continguit fines." Rank heresy! But even the heretic did not venture to reduce a genus having Brown's authority. I believe it was Agardh who said that in his conception Brown was not a man, but SCIENCE. He was a very great botanist, "facile princeps," but *Alsophila* and *Hemitelia* and *Mesochlaena* require more than any authority to justify their permanent recognition.

Hooker, Sp. Fil. I, p. 46, not knowing the plant, at least by this name, said: "It is singular that with so evident an involucre as he describes, Kaulfuss should not have referred this fern to *Cyathea.*"

On a preceding page (21) of the same work, Hooker had already described what has since been regarded as the same species, as *Cyathea beyrichiana* Presl. He there says: "Involucre apparently bursting vertically on the upper side large loose membranaceous persistent at length hemispherical"; and farther down, "In the earliest state of the sorus which has come under my observation, the involucre covers it entirely, but the point of attachment appears to be only on the lower half of the sorus next to the costa."

It remained apparently for Mettenius to combine the two species under *Hemitelia,* wherein he was followed by Hooker and Baker. As Rosenstock noted years ago, and as our many specimens show, the actual indusium is as described by Kaulfuss and then by Hooker.

Alsophila and *Hemitelia* are no more generic entitites in America than in the Orient. *Amphicosmia* is a genus. *Lophosoria* is a genus. *Cnemidaria* is probably to be conserved—the "*Euhemitelia*" of Hooker. But *Alsophila* and *Hemitelia* were both so typified and so described that the attempts to maintain them have never made anything but trouble. At least the great bulk of their species should be recognized as Cyatheas, without the useless compilations of synonyms in the artificial genera. This makes *Cyathea* a most cumbrous genus. It may sometime be possible to break it up along natural lines, but it bids fair to resist this process even more successfully than *Dryopteris.*

It is noted that the dissected basal pinnae of *C. setosa* were not mentioned by Kaulfuss, whose fragment did not include them. Because the fern which bears them is a common one, it is very probable that Kaulfuss' fern was the same, and that the reduction of *Cyathea beyrichiana,* which certainly bears them, is correct.

Cyathea schizolepis Copel. sp. nov.

Plate 3

Cyatheae setosae affinis et similis, pinnis basalibus minutius dissectis carentibus et paleis minoribus distincta; trunco 5 m. alto, gracile, basibusque imis stipitum paleis fulvis anguste linearibus usque ad 12 mm. longis et 0.4 mm. latis castaneo-costatis marginibus pallidis lacerescentibus obtectis; stipite 50 cm. longo, 8 mm. crasso, castaneo, praecipue superne spinis persparsis atrocastaneis 1.5 mm. longis armato, asperulo; fronde 2 m. longa, ovata, profunde tripinnatifida, rhachibus laete castaneis, asperulis; pinna infima (prima) 25 cm. longa, 7.5 cm. lata; pinna ca. sexta maxima, fere 60 cm. longa, 17 cm. lata, stipitulata (2 cm.), brevi-acuminata; pinnulis remotis, medialibus 8.5 cm. longis, 17 mm. latis, sessilibus, acuminatis, costis superne

castaneo-setosis, inferne costulisque et pilis et squamulis fissis pallidis et squamulis rarioribus ramis setaceis castaneis ornatis onustis; segmentis approximatis, 3 mm. latis, obtusis, integris, herbaceis, inferne pallidis minute glanduloso-puberulis; venis plerisque furcatis; soris prope costam instructis, indusio tenue, sorum primo involvente sed mox de apice saepe obliqua disrupto.

Minas Geraes: Viçosa; Fazenda de Aguada, in dense forest, alt. 725 m. *Mexia no. 5059.* Type in Herb. Univ. Calif., nos. 466087 to 466090.

I do not know that this is not *Alsophila setosa* Kaulf., and do not suppose that the question can be decided. It is not the fern commonly known by that name, which is *Cyathea beyrichiana* Presl., from which this differs essentially in the absence of finely dissected basal pinnae, and much smaller and narrower paleae covering the trunk and the bases of the stipes; also, the stipe is more slender and less spiny, the rhachis darker and smoother, and the pinnae more lax and proportionally more slender. The affinity is unusually clear, fixed by the peculiar character of marginate basal scales and still more distinctive costal scales with dark setae.

Alsophila Gardneri Hooker, Sp. Fil. I, 40. 1844

Not *Cyathea Gardneri* Hooker.

In company with several other species, this was later reduced by its author and by Baker (Syn. Fil., 33: Fl. Bras. I II, 329) to synonymy with *A. paleolata* Mart. It is distinguished from that species most conspicuously by being very much more hairy. After its rescue, it still comprises a plurality of forms which in conformity to present usage might be distinguished as species. As described, it is a fern with ''numerous small bullate scales beneath, segments oblong very obtuse entire everywhere clothed with sori. . . . .''

Ferns are described from material the author sees, at best with a little aid from the collector. In the case of tree ferns, the authors of most species not only did not have knowledge of many whole plants, so as to distinguish the features of the individual from those of the race, but never saw one whole plant nor even one whole leaf, and in many cases did not know what part of a leaf they were describing—whether a pinna in hand was from the lower or upper part of the frond. Most tree ferns have the lowest pinnae and the lowest pinnules more or less stalked; almost all have the most distal ones sessile. Many have the lower, more ample segments crenate or toothed, and the smaller distal ones entire. Very commonly the more basal veinlets of the more ample lower segments are forked, while the distal veinlets are almost always simple. From a single frond, a pinna from near the base will be the subject of a description involving stalked leaflets, toothed segments, and forked veinlets, while a pinna from above the middle will be described as different in all of these respects. Likewise one will not conclude from the description of *A. Gardneri* that it never has sterile fronds or partly fertile fronds, nor forget that pubescence may be deciduous. I have a score of Cyatheas which I believe to be new species, which I have so far abstained from publishing, in the hope that more ample material would make possible more competent description.

This is of course not to deny the value of such descriptions as we have, but to point out that they have to be appraised and construed—in the light, if we are fortunate, of more ample material of the same species. Thus *Brade no. 9367,* from Theresapolis, state of Rio de Janeiro, may be accepted as correctly determined, although it shows that the lower portion of the frond may have toothed leaves; which was not to be expected, since the wholly fertile segments of the type were probably from that part of the frond. At any rate, the small bullate scales are fully in evidence on it. Such scales are very nearly wanting on *Brade no. 9737,* from the same place, with entire segments of the pinnules, but serrate pinnule-apex. *Glaziou no. 15775,* from Ouro-Preto, Minas Geraes, conforms to the description. *Glaziou no. 13358,* from Nova Friburgo, Rio de Janeiro, has sharply aculeate rachis of the pinna. It is less hairy than the other specimens cited, but is still *Alasophila Gardneri* rather than *C. paleolata.*

Mexia no. 5175, from Viçosa, is farther from typical than any of the foregoing, in that the bullate paleae are almost wanting. The trunk, according to Mrs. Mexia's field note, is erect, 65 cm. tall and 50 cm. in circumference. The stipe is 120 cm. long, densely fuzzy, but without scales except at the very base where it merges with the trunk; it is covered there with a mat of bright brown, shining, linear-acicular paleae, 2 cm. long, and 2 mm. wide at the base. The stipe bears scattered slender sharp spines, 6 mm. long on its lower part. Decreasing in size, these reach to the rachises of the lower pinnae but not to the upper part of the main rachis. All axes are densely clothed with long brown hairs, which are not very sparse even on the upper surface of the segments. Besides the bullate paleae, a very few longer and plane paleae are detected.

Cyathea Mexiae Copel. sp. nov.

Plate 4

Alsophila, A. Gardneri affinis paleis magnis distinguenda; trunco valido, breve; stipite 60 cm. longo minute fulvo-velutino, ad basin paleis laete brunneis 2 cm. longis 1–6 mm. latis immerso, ubique spinis rectis 2–3 mm. longis acutis horrido; fronde 2 m. longa, 108 cm. lata, profunde tripinnatifida, rhachibus deorsum aculeatis, ibidem breviter velutinis, sursum breviter hirsutis; pinnis stipitulatis (infimis 2 cm.), horizontalibus, acuminatis, basi haud angustatis; pinnulis permultis, infimis brevi-pedicellatis, aliis sessilibus, 6–8 cm. longis, 12–15 mm. latis, basi truncatis, sursum sensim in caudam acutam serrulatam attenuatis, costa inferne dense pilosa cum paleis paucis parvis bullatis sub pilis fere occultis, nec carent omnino paleis brunneis planis 3 mm. longis ovatis; segmentis 2–3 mm. latis, apice oblique rotundatis, papyraceis, inferne hirsutis, superne sparsius pilis rigidioribus, vestitis; venulis ca. 8-paribus, plerisque furcatis nonnulis etiam triramiferis.

Minas Geraes: Viçosa, in cut-over woods on hill southeast of main building of Agricultural College. *Mexia no. 4882,* in Herb. Univ. Calif. nos. 466093 to 466096.

Mrs. Mexia calls attention to the relation of this to her no. 4902, *C. paleolata;* but the nearer affinity is to *Alsophila Gardneri,* her no. 5175, which she recognized as distinct. It is distinguished from the latter by the broad paleae found with the slender ones at the base of the stipe, and by the few large paleae on the costa; from the former by being much more hairy and less scaly; from both, by the very attenuate pinnules.

Cyathea corcovadensis (Raddi) Copel. comb. nov.

Polypodium corcovadensis Raddi, *teste* C. Chr. Index.

Mrs. Mexia has collected no. 4634, with pinnules of the usual form but rather small, and no. 5037, with a part of the material of this type, the pinnae broadly linear with rounded base, but a part of it with pinnae from 5 to 7 cm. long and from 12 to 15 mm. wide and broadly cuneate base. These differ from those of *Alsophila Glaziovii* Baker *non* Fée, as described, Fl. Bras. I II, p. 592, only in not being obviously crenate—and some of them are obscurely so.

Cyathea paleolata (Martius) Copel. comb. nov.

Alsophila paleolata Martius.

Mexia no. 4902.

Cyathea Chamaedendron Copel. sp. nov.

Plate 5

Alsophila, trunco prostrato, 10 cm. vel ultra longa, 2–4 cm. crasso, basibusque stipitum paleis ferrugineis lineari-acicularibus 1.5–2 cm. longis obtectis; stipite usque ad 60 cm. alto, basi 8 mm. crasso atrocastaneo tuberculifero, sursum rhachique stramineis 3 mm. crassis mollibus glabris; fronde 40–45 cm. alta, ovata, acuminata, subcoriacea, glabra (vel mox glabrescente) bipinnata; pinna infirma frondis fertilis 20 cm. longa, 6.5 cm. lata, brevistipitulata (3 mm.), acuminata, pinnulis inferioribus sessilibus, 5 mm. latis, deorsum crenato-lobatis segmento infimo basiscopico aucto, apices suas obtusas versus integris, pinnulis superioribus integris, pinnulis majoribus frondis sterilis serratis; venis pinnatis, venulis utroque latere plerumque 2–3; soris ad venulas dorsalibus nec in lineas instructis, paraphysibus crinitis multis.

Mexia no. 5855a. Minas Geraes, near Diamantina, Fondo do Matador, alt. 1200 m., in streamside jungle. "Only one found." The specimens are actually two, one fertile and one sterile, alike in size. Type in Herb. Univ. Calif. nos. 466105 and 466106.

The obvious first impression made by a dwarf specimen is that it is a juvenile or depauperate individual of a normally larger species. This is not an *Amphidesmium,* which has a normally prostrate stem but with hairs, not scales. In *Cyathea,* too, however, the stem is prostrate at first. The very fully fruiting frond makes it improbable that the specimen in hand is juvenile. Even if a depauperate form of some other species not suspected in this connection, this specimen is related to *Alsophila elegans* Mart. and *A. féeana* C. Chr. The sessile pinnules with rounded apices bar it from both of these; as in these, the margin of fertile pinnules is somehat deflexed. The pinnae and pinnules are non-articulate.

Dryopteris macropoda (Mett.) C. Chr. comb. nov.

Aspidium macropus Mett. Fil. Lechl. 2.20. 1859.

Minas Geraes: Viçosa, Fazenda de Aguada streamside, densely wooded ravine. Frequent. 690 m. *Mexia no. 4915.*

In my Monograph of Dryopteris, I, p. 255, I referred the type of this species leg. Claussen to *D. vivipara.* Mexia 4915 is the same form and it seems to me now sufficiently different from *D. vivipara* by its larger size: pinnae 20 x 3 cm., more deeply crenate-serrulate and whole general appearance.—Note by C. Christensen.

Dryopteris Mexiae C. Chr. sp. nov.

Plate 6

Lastrea rhizomate erecto, paleis brunneis ovatis acutis hirtis sparse obtecto. Foliis caespitosis, stipite ad pinnas evolutas 50 cm. longo, valido, griseo-stramineo, minutissime griseo puberulo, ad basin sparse paleacea. Lamina late ovato-lanceolata, 70 cm. longa, 25 cm. lata, obscure viridi, herbacea, bipinnatifida, rachi breviter et dense griseohirta. Pinnis ad 30-jugis, suboppositis (superioribus alternis), inferioribus vix reductis, abortivis nullis, maximis 15 cm. longis, 25 cm. latis, plerisque breviter (1–2 mm.) petiolulatis, recte patentibus, basi aequaliter truncatis, acuminatis, ad alam 1.5 mm. latam pinnatifidis, costa superne dense strigosa, inferne brevius puberula, laciniis ad 35-jugis parum obliquis, interdum apice subfalcatus, linearibus 10–12 mm. longis, 3 mm. latis, sinu acuto sat angusto separatis, integris, apice antrorsim subacutis, ciliatis, costulis utrinque puberulis, parenchymate utrinque sparsissime setoso cito glabrescente. Venis simplicibus, 16–17-jugis. Soris costulis approximatis, parvis, indusiis minimis dense setosis, sporangiis glabris.

Minas Geraes: Viçosa, Agricultural College, near east boundary, shady gulch at head of watershed, scattered, *Mexia no. 4514,* in Herb. Univ. Calif. no. 419596.

I have some fragments from Caldas (Minas Geraes) collected a century ago by Claussen which probably belong to the same species, differing a little by the larger indusia. By its larger size, great number of veins and subcostular sori different from all Brazilian species known to me, and in general habit more resembling species of the section *Steiropteris.*—Note by C. Christensen.

Blechnum Mexiae Copel. sp. nov.

Plate 7

Lomaria, caudice super terram repente vero 3–4 mm. crasso, basibus stipitum usque ad 1 cm. incrassato, apice adscendente basibusque stipitum paleis fuscis ovatis 5 mm. longis vestitis; stipitibus ca. 5 cm. longis, 1 mm. crassis, fasciculatis; fronde sterile 20–25 cm. longa, 4 cm. lata, utrinque angustata, subcoriacea, pinnata sinubus acutis; pinnis ubique omnino adnatis vix basi dilatatis, medialibus 2 cm. longis, 1 cm. latis, integris, obtusis vel falcato-acutis; frondis fertilis stipite 15 cm. alta, fronde ipsa plerumque breviore, pinnarum paribus inter se 5 mm. remotis infimis remotioribus, pinnis medialibus 2–2.5 cm. longis, 2–3 mm. latis, cuspidatis.

Minas Geraes: Dist. Carangola, trail from Areponga to Fazenda de Grama about kilom. 12, on rain-forest floor, alt. 970 m. *Mexia no. 4237,* in Herb. Univ. Calif. no. 419577. "Long horizontal rootstocks running along ground."

A member of the group of *B. lanceolatum,* distinguished by short, broad pinnae, at most twice as long as broad.

Adiantum gracile Fée

Genera Filicum, p. 116; 7th Mémoire, p. 27, Pl. XI, fig. 1; Christensen, Arkiv för Botanik, 9 (1910) 12. *A. Lancea* var. *gracile* Baker, Flora Brasiliensis I, p. 374.

Mexia no. 6013, from the river Acará, Pará, is doubtfully referred to this variously described species. It was originally described by Fée (Genera, *l.c.*) with "Longeuer totale, 35–38 centim.; la frondule terminale atteint 15 centim.; les latérales sont plus courtes. Les poils qui recouvrent le rachis et le stipe sont laciniés et d'un aspect curieux." These ramose or laciniate scales are indeed peculiar, but imperfectly described in all subsequent publications. Mrs. Mexia's plant is *pergracilis,* and perhaps the tallest of the genus, the stipe of some specimens more than a meter tall, and the blade in one specimen 120 cm. long. This tallest individual has pinnae 35 cm. long by 2.5 cm. wide, and more than 40 pairs of pinnules. Like most of her specimens, it is strictly bipinnate; but a few of them have one to three branches near the base of the lowest one to three pairs of pinnae. The pinnules are broader and rounder at the apex than figured by Fée and described by Baker. The sterile ones are conspicuously cut—agreeing in this detail (unnoticed in other descriptions) with Baker's description: "marginibus exterioribus et superioribus insigniter inciso-serratis."

Polypodium Mexiae Copel. sp. nov.

Plate 8

"Goniophlebium" pilosum aliter P. Catharinae simile; rhizomate valido, 5–7 mm. crasso, repente, paleis brunneis iridescentibus 5 mm. longis basi peltatis 2 mm. latis deinde caudato-acuminatis vestito; stipite gracile, 6–9 cm. longo, stramineo, pube minuta asperso, demum glabrescente; fronde 12–16 cm. longa, 5–7 cm. lata, apice acuta subpinnatifida, basi pinnata, rhachi glanduloso-pubescente; pinnis infimis oppositis, deflexis, adnatis, quam sequentibus paullo minoribus, sequentibus ca. 4 mm. remotis; pinnis medialibus horizontalibus, contiguis vix confluentibus, 3 cm. longis, 1 cm. latis, apice rotundatis, integris, herbaceis, pilis mollibus pallidis utraque facie pilosis et dense ciliatis; venis seriem unam areolarum fertilium includentibus; soris inde prope costam seriatis, superficialibus.

Brazil: Minas Geraes, near Diamantina; serra do Rio Grande, on damp sand under overhanging rock, alt. 1260 m. *Mexia no. 5776a.* Type in Herb. Univ. Calif. no. 466101.

Very similar in general appearance to *P. Catharinae,* but clearly distinguished by the pubescence.

EXPLANATION OF PLATES

All illustrations are photographs by W. C. Mathews, the subjects being type sheets of the respective species. The scale is shown by the millimeter scale on each plate.

PLATE 1

Anemia tripinnata Copel.

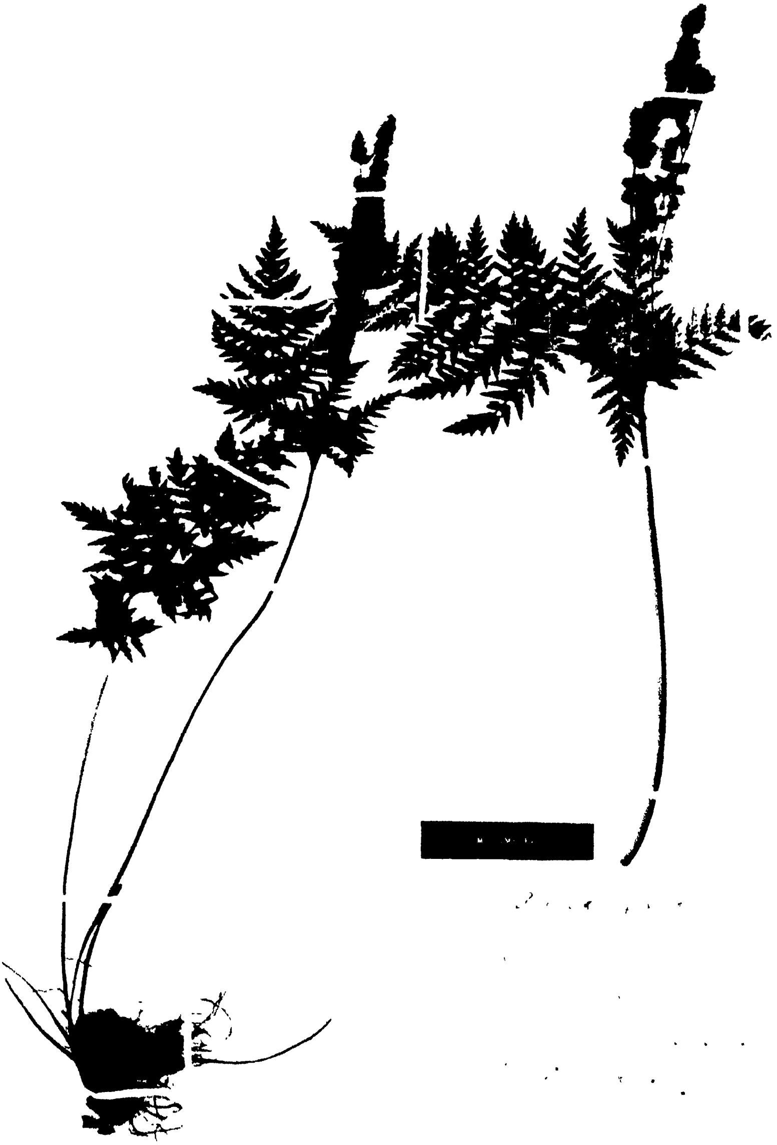


PLATE 2

Cyathea albidopaleata Copel.

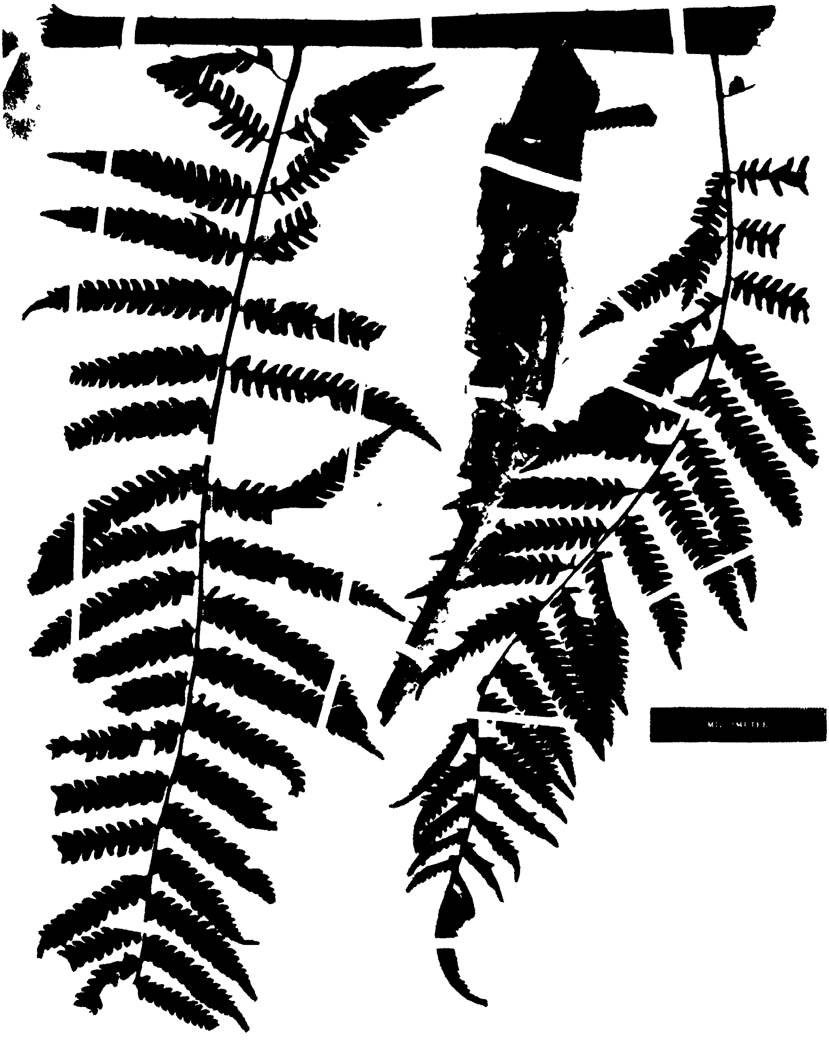


PLATE 4

Cyathea Mexiae Copel.

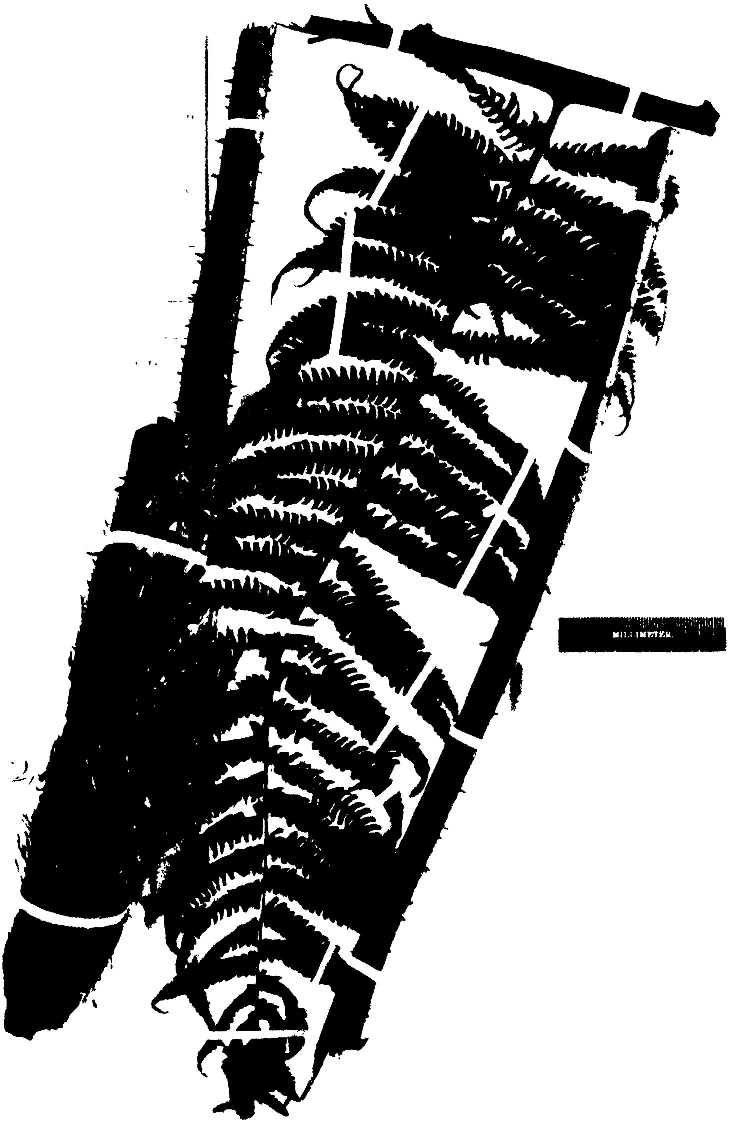

MILLIMETER

PLATE 5

Cyathea Chamaedendron Copel.

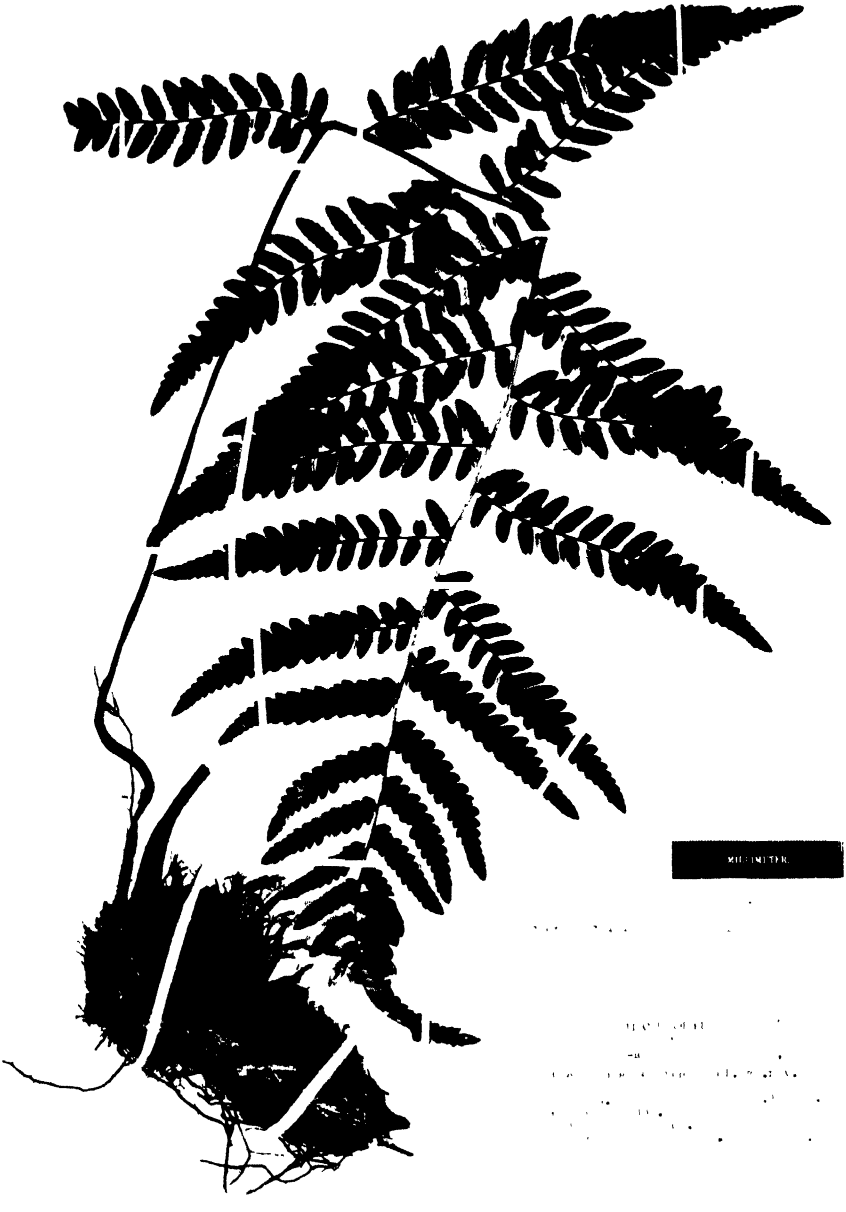

MILLIMETER

PLATE 6

Dryopteris Mexiae C. Chr.

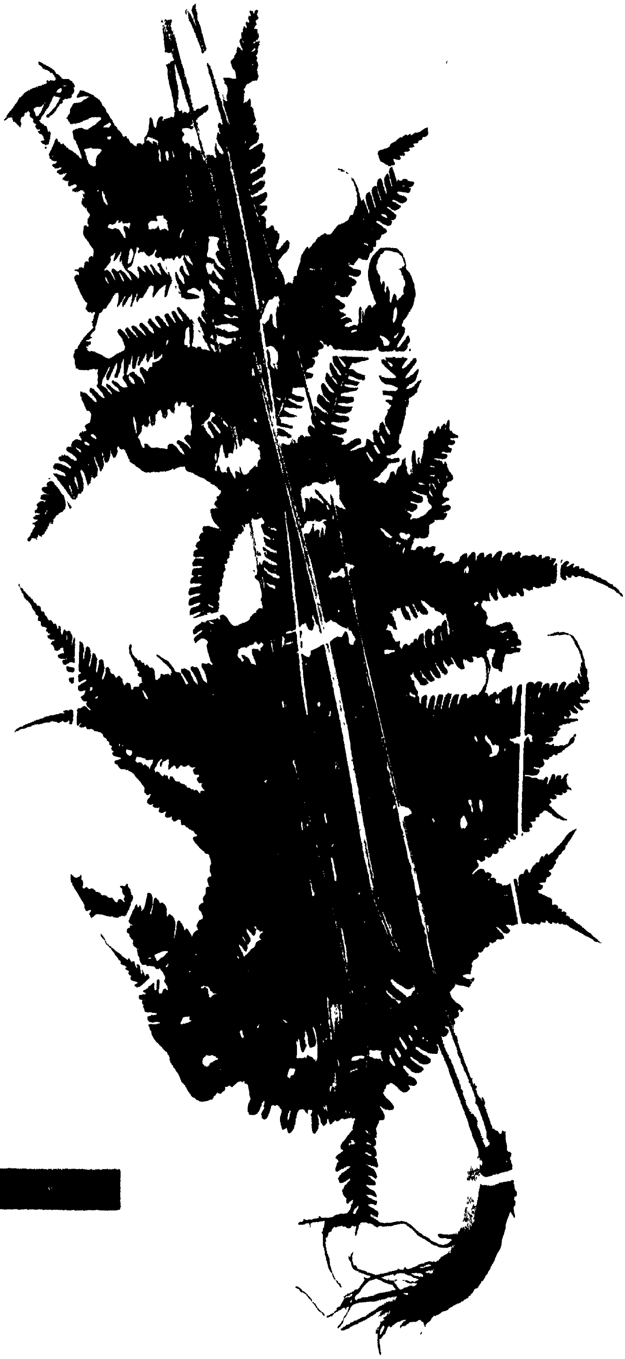
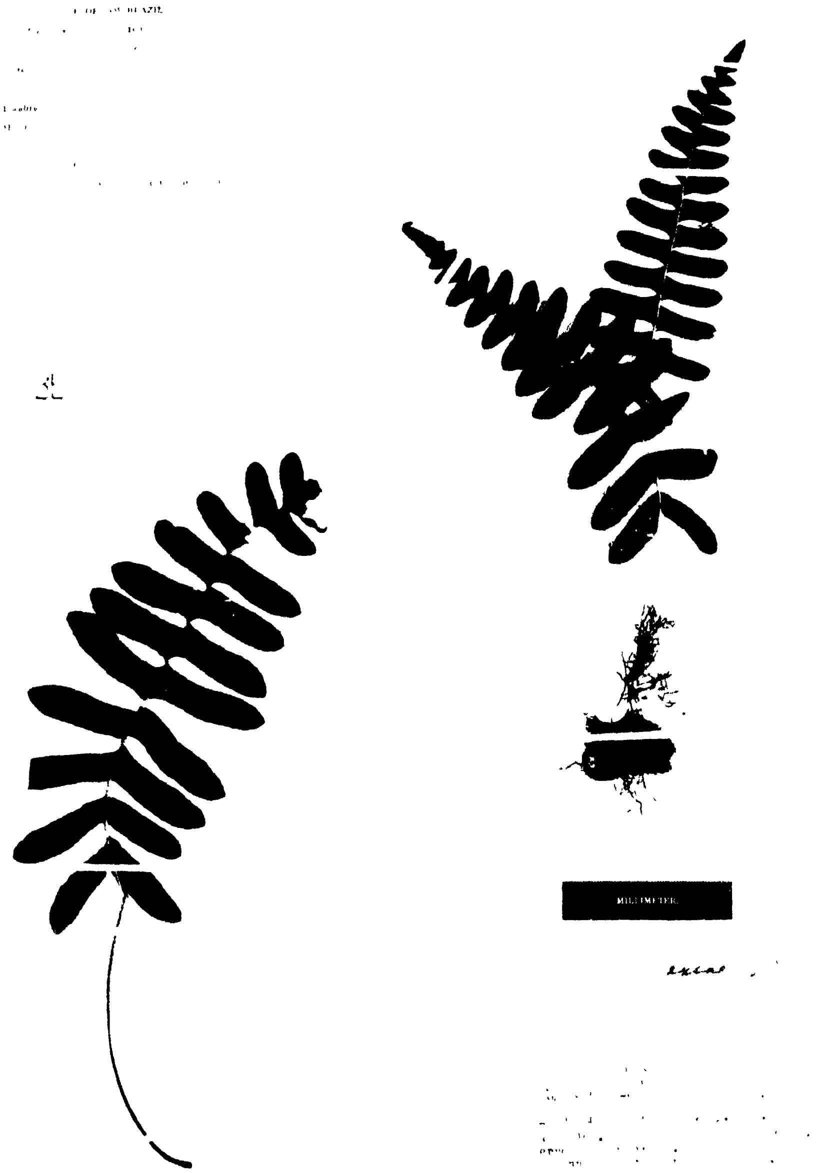


PLATE 8

Polypodium Mexiae Copel.


MILLIMETER

CHROMOSOME VARIATION IN LISTERA OVATA R. BR.

BY

M. MARGARET RICHARDSON

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CHROMOSOME VARIATION IN LISTERA OVATA R. BR.

BY

M. MARGARET RICHARDSON

INTRODUCTION

Listera ovata R. Br. has received a certain amount of cytological attention in the past, and present investigations indicate that it is worthy of closer observation. The earlier workers, both Guignard (1882) and Rosenberg (1905), describe it as containing 16 haploid chromosomes. Müller (1912) reports somatic plates with both 32 and 34 chromosomes. He says "ebenso haufig wie 32, fand ich bei meinen Zahlungen, 34 chromosomen." Hoffmann (1930) found $n = 17$, of which there were 14 small ellipsoidal and approximately similar in size, and 3 strongly bent bigger chromosomes in the heterotype metaphase plates. He never found $n = 16$ as reported by the previous workers. Tuschnyakova (1929) has helped considerably to clear up the problem presented by this species. She found a reduced number of 17 chromosomes but says—"auf 500 gameten mit 17 chromosomen wurden 4–5 mit 18 und etwa ebenso viel mit 16 chromosomen gefunden." She reports that the haploid chromosome set of $n = 17$ is characterized by having the following types of chromosome:

3 large (One 'S'-shaped and two hook-shaped),
2 medium sized,
12 quite small, often with medium construction.
In the 16-chromosome gamete, a medium sized chromosome was lacking, while an additional small one was present in the 18-chromosome set.

From her study of meiosis she was able to assign the cause of the aberrant numbers to "non-disjunction." This phenomenon was seen by her, occurring not only during the meiotic process in macrospore and microspore mother cells, but also in the first division of the primary nucleus of the pollen grain. She describes the manner in which a bivalent on the heterotype plate may fail to divide, and may either go to one of the poles where it becomes submerged with the univalents, or remain on the spindle. In the former case gametes are subsequently formed with unequal numbers of chromosomes; namely, 16 and 18. With the latter, small, supernumerary nuclei are produced which are persistent within the tetrad.

She postulates the appearance of plants with 32, 33, 34, 35, and 36 chromosomes, but declares that, although she has investigated root tips from many individuals, in no case could she find a somatic count other than 34. In one of Müller's preparations, however, she saw plates with 36 chromosomes. It is significant in this respect that Müller illustrates a plate with 36 chromosomes but fails to remark about it.

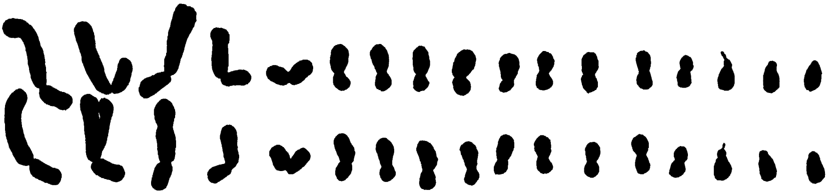

Fig. 1. *L. ovata* No. 7729. Somatic chromosome complement $2n = 34$.

The present observations confirm Tuschnyakova's postulated somatic chromosome numbers of 35 and 36, and also indicate that fragmentation occurs in this species. Further attention has been paid to chromosome morphology, and the presence of satellites is noted for the first time.

The plants in this investigation were collected in England, and it is unfortunate that no material was available for the study of meiosis, so that this aspect of the problem must be left until later.

METHODS

The root tips were fixed by Langlet's chrome-acetic formalin solution, and stained by Haidenhain's iron-alum haematoxylin method. Sections were cut at thicknesses of 14 and 16μ. Drawings were made at bench level using a Leitz 1.30 mm objective, a 15x eyepiece, and a tube length of 170 mm to give a magnification of × 3000 with a camera lucida. Fig. 1 was drawn at a slightly higher magnification. In reproduction the drawings are reduced one-half.

OBSERVATIONS OF CHROMOSOME VARIATION

7729 Unknown locality in Northumberland.

This plant had 34 clearly defined somatic chromosomes. A great number of plates in roots of one individual were examined and in no case were fragments discernible. There was a great range of size of chromosomes in the complement, the largest being approximately six times as long as the smallest. The following chromosome types are present (see fig. 1).

(1) 3 pairs, large, with submedian constriction; one pair appears to be slightly larger than the other two, its shorter arm is longer, and it would seem that there is a seat of weakness two-thirds of the distance from the attachment constriction along the length of the longest arm, since the end is frequently very strongly bent.
(2) 1 pair, smaller, with submedian constriction.
(3) Still smaller, 13 pairs, among which the following types may be distinguished:
  a. Median attachment constrictions.
  b. Submedian attachment constrictions.
  c. Terminal attachment constrictions, on the three smallest pairs, of which one pair bears a small satellite attached to the end with the constriction.

These 26 small chromosomes show a slight range in size, but they are all very appreciably smaller than the two other types.

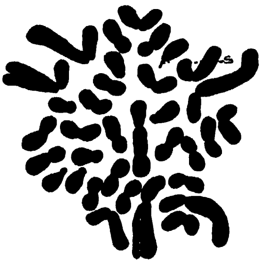

Fig. 2

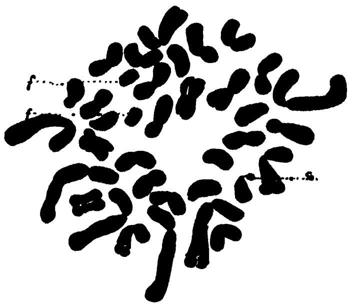

Fig. 3

Fig. 2. *L. ovata* No. 7729. Thirty-four chromosomes. × 1500.

Fig. 3. *L. ovata* No. 1731. Thirty-six chromosomes, two fragments, and one satellite are visible. × 1500.

1731 Blackhalls Durham.

This individual was found to have 36 chromosomes. The complement appeared to be entirely similar to that of the plant just previously discussed with the following exceptions:

(1) The addition of two very small chromosomes or fragments with no visible attachment constrictions and with blunt ends, giving them the appearance of small rectangular bodies (see fig. 3). They are approximately half the size of the smallest chromosomes.
(2) One of the small chromosomes with a terminal attachment constriction bears a large satellite, and the pair of satellited chromosomes in 7729 is absent. A search was made to see whether there were two such satellited chromosomes in the complement, but the paucity of material prevented a definite decision on this point.

7631 Dilston.

This specimen also had 36 somatic chromosomes. Two chromosomes with satellites, of the same type as described above for 1731, were clearly visible. In all other respects the chromosome complement seems to be identical with that of 1731, and the same small pair of fragmented chromosomes is present (see fig. 3).

7530 Dilston.

In the root tips of this individual 36 somatic chromosomes are present. The complement differs from those of 1731 and 7631 in that there are apparently no satellited chromosomes. In all other respects the chromosomes are quite similar and the same two small fragments are seen (see fig. 4).

7531 Dilston.

This plant was aberrant in having three leaves instead of only two. On investigation it was found to contain 35 somatic chromosomes. Only one of the small fragmented chromosomes is present, and only one satellited chromosome of the type in 1731 and 7631 was seen in the plates. For the remainder, the chromosomes seemed to have the same morphology as in the other individuals (see fig. 5).

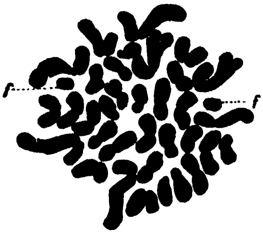

Fig. 4

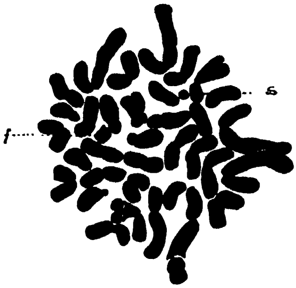

Fig. 5

Fig. 4. *L. ovata* No. 7530. Thirty-six chromosomes, two fragments are present.
Fig. 5. *L. ovata* No. 7531. Thirty-five chromosomes, one fragment, and one satellite are present. Both figures × 1500.

It had been intended to secure some measurements on the lengths of the arms in the larger chromosomes, in order to see whether any relationship might be established between these lengths and the presence of the small fragmentary chromosomes, but this proved impossible owing to the fact that the long arms were very frequently not flat on the equator of the spindle, but extended toward the poles.

DISCUSSION

The satellite.—The presence of the satellite has not hitherto been reported in this species, and with the exception of *Epipactis falcata* (Sugiura 1930) it has not yet been found in any member of the Orchidaceae. M. Navashin's (1925) work on *Crepis* has shown the variability that may exist within the confines of a species in regard to the form of the satellite, and since then many other instances have been reported in the literature. These have been demonstrated in naturally occurring material or have been artificially induced as a result of X-ray treatment.

It is evident that there is some form of chromosome change operative in *Listera ovata* which has given rise to the previously discussed forms in which the satellite is apparently lacking (7530), or if it is present, it is so close to the end of the chromosome, and to the two different masses of chromatin in the satellite as to be invisible. In all cases the chromosome bearing the satellite has similar morphology; namely, it is one of the smallest chromosomes in the complement, and it has a terminal attachment constriction, the satellite being attached to this end (see figs. 1, 4).

Fragmentation.—Tuschnyakova (1929) demonstrated the addition of a small chromosome to the haploid complement of 17, thus yielding a gamete with 18 chromosomes. This is in accordance with the present observations in which the 36-somatic complement gains two small chromosomes. She ascribed the additional chromosome to the non-disjunction of a small bivalent, and postulated the occurrence of individuals with 36 chromosomes through the fertilization of two 18-chromosome gametes. If such were the case, however, the two additional small chromosomes should be similar in morphology to one of the small chromosomes in the 34-diploid complement. Such is not the case. It has been demonstrated that the two small chromosomes gained by the individuals with 36 chromosomes are appreciably smaller than the other chromosomes in the complement, and furthermore that they are different in morphology. Their blunt ends and the absence of any visible attachment constriction would incline to the hypothesis that they have arisen through fragmentation. Fragmentation has been extensively studied in other genera, as for example *Zea* (Randolph 1928), *Crepis* (Navashin 1925), and by Darlington on *Tradescantia* and *Fritillaria* (1929). The last author found that the fragments arose during the prophase of meiosis; and that they were capable of forming new attachment constrictions. Their survival and subsequent behavior was dependent on this faculty for mitotic perpetuation, and on their ability to form chiasmata during meiosis; otherwise degeneration ensued.

In the absence of evidence concerning the meiotic behavior of these different chromosomal forms of *Listera ovata,* speculation is somewhat futile as to whether they have arisen through fragmentation, or as the result of non-disjunction of a small bivalent, as Tuschnyakova believes, but there are three significant features which would seem to support the fragmentation hypothesis; namely,

a. Their dissimilarity in morphology with any of the chromosomes in the 34-somatic complement (see illustrations).

b. The relatively large size of the satellite in 1731 and 7631 would seem to indicate that chromosome breakage is occurring in the species.

c. The large range in size shown by the somatic chromosomes, more especially the sharp difference between the three large pairs and the remaining ones, would seem to indicate that the smaller chromosomes have been derived from the larger ones by breakage, rather than that the larger ones have been derived by fusion of two smaller ones, since the long arms of the large chromosomes are longer than any of the small ones.

Chromosome number.—The impression hitherto current that a species is characterized by a single invariable chromosome number, is now no longer accepted. J. Clausen (1931) has summarized the evidence in this respect, and since then further examples have been reported. There are those species in which the chromosome number is constant within a variety, and very frequently the numbers are in a polyploid series. In such cases they have probably arisen through tetraploidy with subsequent intraspecific hybridity, and diversity in chromosome number may, or may not, be accompanied by a difference in external morphology. *Listera ovata* belongs to the category of species with an oscillating chromosome number. It has been demonstrated that in this species there are naturally occurring forms with 32, 34, 35, 36 somatic chromosomes, Examples of this class are found in *Viola canina* (J. Clausen 1931) with $2n = 40$ plus a varying number of fragments and chromosomes, and in *Crepis syriaca* with $2n = 10, 11, 12, 13, 14, 15, 16, 18$ (Hollingshead and Babcock 1930) and Cameron (unpublished. In neither are the conditions quite analogous to those in *Listera ovata.* V. canina is thought to be a hypertetraploid which maintains itself through intercrossing within the species, and that it renews itself through outcrossing with a related species. In *Crepis syriaca* the variability is ascribed to hybridization between two forms of a related species, *C. alpina,* followed by chromosomal modifications (Cameron). In *Ranunculus acris* the variation in chromosome number is postulated by Sorokin (1927) to result from crosses between different polyploid forms. In *Listera ovata* we have no evidence as to whether we are dealing with a polyploid species, as this is the only species in the genus whose chromosome number is known. It is improbable that recent interspecific hybridity has been effective in the production of these forms, since there are only two species of *Listera* in Great Britain, and these two occupy widely differing habitats. Furthermore, as yet no polyploid races have been described in this species, so that the suggested explanation for the phenomenon in *Ranunculus acris* will not hold here, although intraspecific hybridity between a form such as 7729 with $2n = 34$ and a form with $2n = 36$, as Tuschnyakova suggests, has probably led to the production of 7531 with 35 somatic chromosomes. It is significant that this individual (7531) has only one satellited chromosome and one small fragmented chromosome in its complement. This is the expected result from a cross between a form like 7729 and 7631. The problem is one that requires further investigation before a more definite explanation is offered, although the present evidence would not seem to be in complete agreement with Tuschnyakova's hypothesis.

The genetic aspect of the phenomenon is not without interest, for the addition of two small fragmented chromosomes has not apparently upset the balance within the genom to such an extent as has the presence of only one small chromosome in 7531 with $2n = 35$, where there are three leaves instead of the normal two. Furthermore, this may be tentatively postulated to be a reversion to a more primitive condition, since the remainder of the Orchidaceae are characterized by more than two leaves.

SUMMARY

1. Material of *Listera ovata* collected in the field is found to exhibit variation in chromosome number. Normal individuals are observed with either 34 or 36 somatic chromosomes, and one aberrant plant with three leaves contains 35 chromosomes.

2. The numbers 35 and 36 afford confirmation of Tuschnyakova's hypothesis, but the evidence from chromosome morphology is not in complete agreement with her attributed cause.

3. Satellites are demonstrated to be present in this species.

4. Fragmentation is discussed as a possible cause of variation in chromosome number.

ACKNOWLEDGMENTS

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CYTOLOGICAL AND MORPHOLOGICAL STUDIES IN THE GENUS FICUS

II. CHROMOSOME NUMBER AND MORPHOLOGY IN THIRTY-ONE SPECIES

BY

IRA JUDSON CONDIT

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CYTOLOGICAL AND MORPHOLOGICAL STUDIES IN THE GENUS FICUS

II. CHROMOSOME NUMBER AND MORPHOLOGY IN THIRTY-ONE SPECIES

BY

IRA JUDSON CONDIT

INTRODUCTION

In a previous paper (Condit, 1928) the writer reported upon the chromosome number and morphology in seven species of the genus *Ficus*. The diploid chromosome number of six species, viz., *carica* L., *pseudocarica* Miq., *palmata* Forsk., *elastica* Roxbg., *rubiginosa* Desf., and *erecta* Thunb., was determined to be 26 each, the morphological characters of the chromosomes in the different species being very similar. The chromosomes of *F. glomerata* Roxbg. appeared to be 24 in number and were found to be different in size and shape from the chromosomes of the other six species.

Krause (1930) has recently made cytological studies of several species of *Ficus* and confirms my report that the somatic chromosomes of *F. elastica* number 26. He found (see also Tischler, 1931) that in *F. altissima, F. pandurata,* and *F. parcelli,* the diploid chromosome complement is 26; that in *F. quercifolia* there are 28 chromosomes; that in *F. panduraefolia, F. schlechteri, F. sycomorus,* and *F. triangularis* there are probably 26 somatic chromosomes each, and that in *F. bengalensis* and *F. repens* the diploid set of chromosomes probably numbers 28 in each species. Tischler (1931) lists the chromosome numbers of the various species of *Ficus* so far determined and records, "*Ficus palmata* (*pseudocarica*)." Both *F. palmata* and *F. pseudocarica* are being grown to some extent commercially in California as a source of caprifigs. They are closely related but specifically distinct both in fruit and foliage characters. Tischler's list does not name the authors for the species mentioned. If the *F. repens* included in the list is the common "Creeping Fig" of gardens, it is now usually listed in botanical indexes as *Ficus pumila.*

The present paper deals with the chromosome number and morphology of thirty-one species of *Ficus* including four studied by Krause

(1930). The identity of each species has been checked with various botanical descriptions, and by comparison with herbarium material at the University of California, Berkeley.

MATERIALS AND METHODS

Plants of the species of *Ficus* in the present collection have been obtained from botanical gardens, commercial firms, or collaborators in various parts of the world.

Root tips from potted plants were fixed 12–24 hours in Karpechenko's solution made up as follows:

Solution A

Water	65 cc.
Glacial acetic acid	10 cc.
Chromic acid	1 gram

Solution B

Water	35 cc.
Commercial formalin	40 cc.

Equal quantities of solutions A and B are mixed immediately before placing the material in the killing fluid.

After embedding in paraffine, sections were cut 6 microns in thickness and stained in Haidenhain's iron-haematoxylin. The use of butyl rather than ethyl alcohol, as suggested by Zirkle (1930), materially shortened the dehydration period preceding embedding in paraffine and proved thoroughly satisfactory.

CLASSIFICATION OF SPECIES OF FICUS

The genus *Ficus*, includes over 600 species widely scattered over the tropical and subtropical regions of the world. To it belong such extremely diverse forms as the common fig, the sycamore fig, the banyan tree, various strangling figs, the rubber tree, the creeping fig, the Moreton Bay fig, the peepul tree, and many others. Over 150 fossil species are listed by Knowlton (1919) from North America indicating that the genus was once widely distributed over this continent as far north as Alaska.

The Asiatic species are classified by King (1887) as follows:

Group 1. Pseudo-hermaphrodite: male flower with one stamen and a rudimentary pistil .... *Palaeomorphe*
Group 2. Unisexual or asexual: male flower without rudimentary pistil.
  Section 1. Male, gall, and fertile female flower on the same receptacle.... *Urostigma*

Section 2. Flower unisexual or neuter: male and female flower on one set of receptacles, fertile female and neuter flowers on another set..................*Synoecia*

Section 3. Flower unisexual: male and gall flower in one set of receptacles, fertile female flower only in another set.

- *A.* Flower monandrous
  - *a.* Receptacles chiefly axillary..*Sycidium*
  - *b.* Receptacles mostly in fascicles from stem and branches.....................*Covellia*
- *B.* Flowers di- rarely triandrous
  - *a.* Receptacles mostly axillary ....*Eusyce*
  - *b.* Receptacles mostly in fascicles from stem and branches..............*Neomorphe*

The above classification is widely used by botanists in describing species of figs. Most of the species studied cytologically during the course of the present investigation will be listed according to King's classification. One species is included in the group Bibracteatae, one in Pharmacosyce, while some are unclassified.

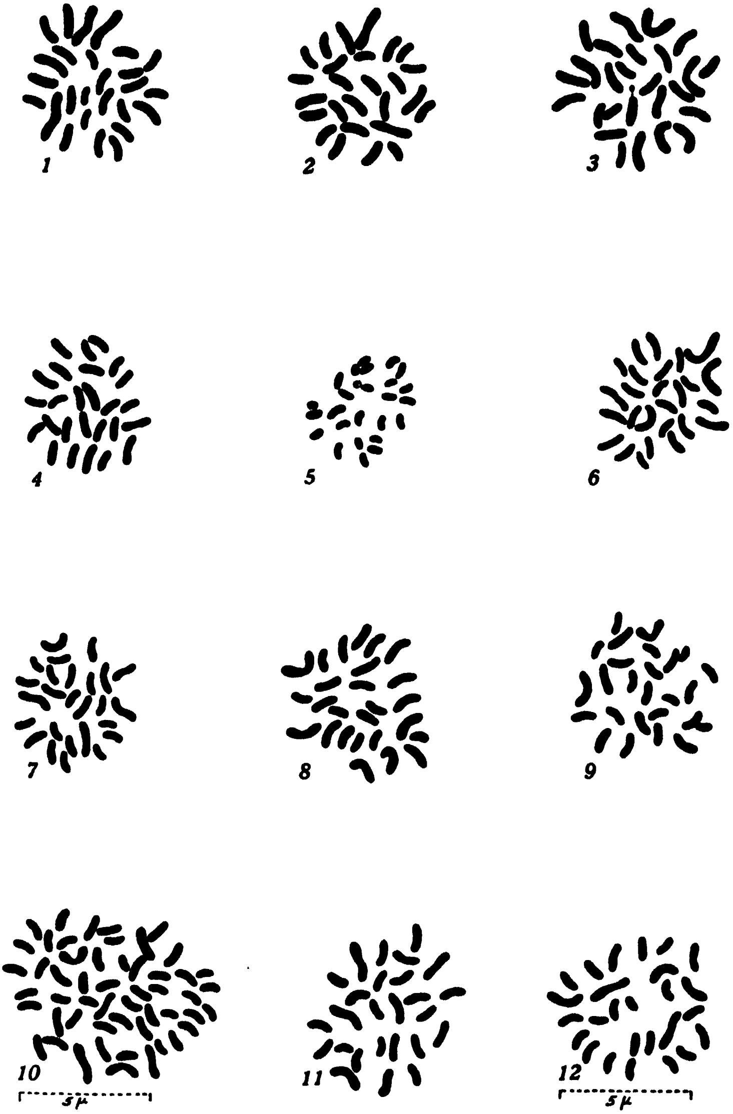
GENUS FICUS

CHROMOSOME NUMBER AND MORPHOLOGY

The chromosome complements of the different species of *Ficus* differ considerably in clearness and sharpness of outline, depending undoubtedly on the condition of the material when fixed as well as on certain variations in technique. In the most favorable preparations the chromosomes appear distinctly black against the gray cytoplasm. Most species show metaphase plates in which the chromosomes are well spaced in a single plane, although good photographic reproduction is seldom possible.

The chromosomes of the various fig species are similar to one another in appearance, but show certain morphological characters which are more or less distinctive. The individual chromosomes are exceedingly small. The size range in the chromosomes of the common fig has been found (Condit, 1928) to be from considerably less than 1μ to a little over 2μ in length, the length of the larger individuals being several times greater than the diameter. These measurements apply approximately to the chromosomes of *F. pandurata* shown in figure 13 of this paper and to those of various species illustrated in figures 1–12.

By contrast reference can be made to Darlington's table (1932, p. 85) giving the range in size and number of chromosomes in various species. The chromosomes of *Drosera capensis* are 1.0μ in length, while those of *Drosophyllum lusitanicum,* another genus of the Droseraceae, are 25μ long. Both *Prunus laurocerasus* and *Oenothera biennis* show short chro-



Figs. 1–12. Somatic chromosomes of fig species, drawn from root-tip cells in the metaphase of mitotic division, polar view.

All drawings were made with the aid of a camera lucida and a Zeiss microscope equipped with an apochromatic H I 90 oil immersion objective, numerical aperture 1.3 and a planoscopic 20 × eyepiece. Magnification approximately 3050.

1. *Ficus benjamina crassinervia*
2. *Ficus eugenioides*
3. *Ficus henneana*
4. *Ficus religiosa*
5. *Ficus religiosa*
6. *Ficus watkinsiana*
7. *Ficus asperrima*
8. *Ficus diversifolia*
9. *Ficus pumila minima*
10. *Ficus pumila minima* (tetraploid)
11. *Ficus glomerata*
12. *Ficus subscabrida*

mosomes, 2.5μ in length. At the other extreme are hyacinth chromosomes, 21μ long. The chromosomes of certain species of *Crepis* (Hollingshead and Babcock, 1930) range from 2 to 10μ in length, while some of *Nicotiana alata* (Ruttle, 1927) are 6 or 7μ long. Randolph (1928) found that in 20-chromosome plants of *Zea mays* the shortest chromosomes were approximately 2μ in length and the longest about 4.5μ.

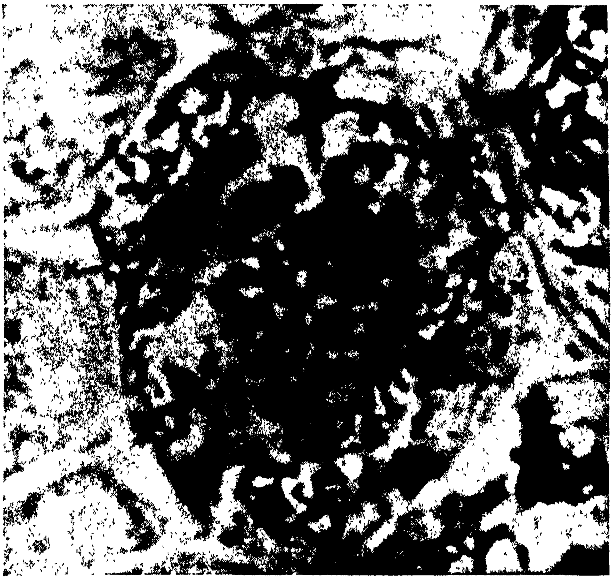


Fig. 13. Chromosomes (*2n=26*) from root-tip preparation of *Ficus* pandurata, × 3450. The three units marked "x" consist, in each case, of two Chromosomes.

The morphology of fig chromosomes depends upon their length and upon the position of their spindle fiber attachments. Sub-median attachments account for the *J*-shaped chromosomes described and figured here and in a previous paper (Condit, 1928). Median fiber attachments account for the falcate chromosomes and for the *V*- or *U*-shaped chromosomes shown in figures 3, 6, 8, 9, and 10, the latter appearing to be characteristic of certain species. In two species, *F. henneana* and *F. mysorensis,* a conspicuous appendage on certain individual chromosomes indicates that a pair of satellited chromosomes is characteristic of their somatic cells. It is an interesting coincidence that fig chromosomes are the same in number as the chromosomes of three species of *Luffa* figured by McKay (1931), with which they also share similar morphological characters.

TABLE 1

Chromosome Counts of 43 Species of Ficus

Species	Number *N*	Number *2N*	Authority
altissima Blume	13		Krause* 1930
		26	Author
asperrima Roxbg.		26	Author
bengalensis Linn.	14(?)		Krause* 1930
		26	Author
benjamina Linn. var. *crassinervia*		26	Author
calophylloides Elm.		26	Author
carica Linn.	13	26	Author 1928
carica Linn.		26	Author 1932
cumingii Miq.		26	Author
diversifolia Blume		26	Author
elastica Roxbg.		26	Author 1928
		26	Krause 1930
erecta Thunb.		26	Author 1928
eugenioides F. Muell.		26	Author
glabella Blume		26	Author
glomerata Roxbg.		24(?)	Author 1928
glomerata Roxbg.		26	Author
henneana Miq.		26	Author
indica Linn.		26	Author
macrophylla Desf.		26	Author
mitrophora Warb.		26	Author
mysorensis Heyne.		26	Author
nigens (?)		26	Author
palawanensis Men.		26	Author
palmata Forsk.	13	26	Author 1928
palmata Forsk.		26	Author 1932
payapa Blanco		26	Author
panduraefolia Vill.		26	Krause 1930
pandurata Hort.	13		Krause* 1930
pandurata Hort.		26	Author
parcelli	13		Krause* 1930
platypoda A Cunn. var. *petiolaris* Benth.		26	Author
populnea Willd. var. *brevifolia* Warb.		26	Author
pseudocarica Miq.		26	Author 1928
pseudopalma Blanco		26	Author
pumila Linn.		26	Author
pumila Linn. var. *Minima* Hort.		26	Author
quercifolia	14		Krause* 1930
religiosa Linn.		26	Author
repens	14(?)		Krause* 1930
retusa Linn.		26	Author
rubiginosa Desf.		26	Author 1928
scabra G. Forst.		26	Author
schlechteri		26	Krause 1930
sp. (*issi*)		26	Author
subscabrida Warb.		26	Author
sycomorus	13(?)		Krause* 1930
triangularis	13(?)		Krause* 1930
ulmifolia Lam.		26	Author
vogelii Miq.		26	Author
watkinsiana Bailey		26	Author

* Listed by Tischler (1931) as "Unveroffentl. Angaben betr. Urticales," Krause 1930.

Table 1 lists the forty-three species of *Ficus* in which chromosome counts have been made, the chromosome number of each, and the authority for the determination. The following is a more detailed account of cytological studies of root-tip material representing thirty-one species of *Ficus*.

SUBGENUS UROSTIGMA

In all the species of the subgenus *Urostigma* studied in this investigation the diploid chromosome number is 26. The chromosomes of *F. altissima, F. bengalensis, F. benjamina* var. *crassinervia* (fig. 1), *F. calophylloides, F. eugenioides* (fig. 2), *F. indica, F. macrophylla, F. mitrophora, F. palawanensis, F. payapa, F. retusa* are similar morphologically to those of *F. carica.* These counts confirm the determination for *F. altissima* made by Krause (1930) but the number is two less than the probable chromosome number given by him for *F. bengalensis.*

A pair of broadly *V*-shaped chromosomes appears to be characteristic of *F. henneana* (fig. 3) while in several metaphase plates a single satellite-bearing chromosome is distinctly in evidence. More careful destaining of other material is expected to show a pair of chromosomes each having an appendage. A pair of *V*-shaped chromosomes is also found in *F. mysorensis* and an occasional conspicuous appendage indicates a pair of satellited chromosomes for this species. Two strongly curved or nearly *U*-shaped chromosomes are present in most plates of *F. platypoda* var. *petiolaris.* One species was received as *F. brevifolia* but according to Warburg (1903) this is a variety of *F. populnea.* The larger chromosomes of this species are slightly curved but not of such characteristic shapes as found in some other species.

In *F. religiosa* the division figures in the material examined were all in the plerome; as usual in this case the chromosomes are rather densely clustered together and the individuals are shorter and thicker (fig. 4) than in division figures of the periblem. In one root-tip preparation of this species the chromosomes are globular or reniform (fig. 5) somewhat similar to those of *F. glomerata* figured by Condit (1928). Two chromosomes of *F. watkinsiana* are *U*-shaped verging into *V*-shaped while the chromosomes of another pair are shaped somewhat like a *J* (fig. 6). The chromosomes of *F. glabella* are shorter and thicker than those of most other fig species studied.

SUBGENUS SYCIDIUM

In the following species of the subgenus *Sycidium,* 2n=26. The division figures in material of *F. asperrima* are unusually clear and the chromosomes especially well defined, some of the individuals being strongly curved but not distinctly *V*- or *U*-shaped (fig. 7).

Two plants received as *Ficus* sp., have been identified as *F. cumingii* by Dr. S. F. Blake, Washington, D. C. The chromosomes of this species are shorter, thicker, and more uniform in size and shape than are those of most other species. In *F. ulmifolia,* strongly curved to *V*-shaped chromosomes are present in some metaphase plates and are probably characteristic of the species.

SUBGENUS EUSYCE

In five species of the subgenus *Eusyce,* 2n= 26. *F. diversifolia* shows a pair of chromosomes each *J*-shaped, also two *V*-shaped chromosomes.

In one list of Philippine figs, Elmer (1907, p. 202) includes *F. pseudopalma* in the subgenus *Eusyce,* while in another list (1907, p. 257) he places it in *Covellia.* A plant received from Florida as *F. villosa* appears to be identical to *F. pumila,* the common ''creeping fig'' of California gardens, and is included in the above list as *F. pumila.* In *F. pumila* var. *minima,* a small-leaved form of the ''creeping fig,'' a pair of *V*-shaped chromosomes is found (fig. 9). A single cell of meristematic tissue with a tetraploid number of chromosomes is present in this preparation (fig. 10), the first tetraploid cell so far recorded in any *Ficus,* although a polyploid and euploid condition is reported (Condit 1932) in the endosperm cells of *F. carica* and *F. palmata.*

The chromosomes of *F. scabra* are similar morphologically to those of *F. carica* and of various other species.

SUBGENUS NEOMORPHE

The species *F. glomerata* is placed in the subgenus *Neomorphe* by King (1888) and in *Covellia* by Bailey (1909). Material from three different sources, examined during the course of the present investigation, shows in each of twenty-five plates, 26 somatic chromosomes similar in general shape and size to those of *F. carica* and of various other species studied (fig. 11).

One root-tip preparation of *F. glomerata* previously studied (Condit 1928) showed globular or oblong chromosomes probably 24 in number located in the periblem. Similar chromosomes are found in the plerome in one preparation of *F. religiosa* as mentioned above. The strikingly different forms of somatic chromosomes in these two species indicate the necessity of carefully noting the individuality of the plant and its condition at the time root tips are taken. Lammerts (1929) found that division figures of older *Nicotiana* roots exhibit shorter and thicker chromosomes than those of younger roots. Rybin (1927, p. 224) found the somatic chromosomes of a heteroploid hybrid *Nicotiana* to be strikingly shorter and thicker in the region of the root cap than in the periblem. The age factor may account for the peculiar chromosomes in certain preparations of these two species of *Ficus.*

SECTION *PHARMACOSYCE* MIQ.

The preparations of *F. subscabrida* are unusually good, the twenty-six chromosomes being widely spread apart and sharply defined (fig. 12). This species is placed in the section *Pharmacosyce* by Warburg (1903).

SUBGENUS BIBRACTEATAE

F. vogelii (2n=26) is included in the subgenus *Bibracteatae* by Mildbraed and Burret (1911).

UNCLASSIFIED SPECIES

F. nigens (2n=26) is a South African species received as seed.

In *F. pandurata*, 2n=26, confirming the count reported by Krause (1930). This species is characterized by a pair of strongly curved or almost *V*-shaped chromosomes. Of the hundreds of metaphase plates studied during the course of this investigation, one plate was found in this species in which the chromosomes are sufficiently spread out in a single plane to make photographic reproduction practicable (fig. 13).

A plant from Hawaii, received as *Ficus* sp.–(issi) (2n=26), has not been specifically determined. The term ''issi'' might refer to any one of several different fig species of the Philippines.

DISCUSSION

For a genus which has such a wide diversity of plant forms it is rather unexpected to find in *Ficus* such a uniformity in chromosome number and morphology. Other investigators, however, have discovered a similar cytological condition to exist in certain genera. For example Sax (1930) as the result of his study of some 15 species of *Rhododendron*, expresses surprise to find the chromosome number so constant, in view of the fact that the species of the genus show such a great variation in form and in geographic range. Although McKay (1931) finds in the *Cucurbitaceae* a considerable range of chromosome numbers he reports a striking uniformity of size and shape of chromosomes and regards this as unusual considering the great amount of diversity exhibited by the species examined.

On the other hand published lists of chromosome numbers show that it is fairly common in plant genera for the numbers to be uniform or nearly so. In his cytological examination of *Philadelphus,* including 21 species, 2 varieties, and 12 hybrids, Bangham (1929) shows that all have a haploid complement of 13 chromosomes which appear to be perfectly compatible in the hybrids. Miss Blackburn (1928) lists 46 species of *Silene* all but two of which have 12 as the haploid chromosome number. In over 80 species of two groups of the *Caryophyllaceae* she finds that the form of chromosome at the reduction division is most remarkably constant. In connection with his study of the chromosome complement in *Ribes,* Darlington (1929) thinks it significant that in the three genera, *Rubus, Prunus,* and *Ribes,* each of which is remarkable for the freedom with which hybridization occurs between forms morphologically distinct, there should be a striking constancy of chromosome form and a regularity of chromosome number. Other large genera in which the chromosome number is constant or nearly so are *Linaria, Quercus, Medicago,* and various genera of the Liliaceae.

Based on the cytological studies, in 43 out of the 600 or more species in the genus, the series of chromosome number in *Ficus* is evidently of the *Antirrhinum* type (Tischler 1928) although Krause (1930) reports one fig species with 28 somatic chromosomes. In the *Antirrhinum* type the chromosome number does not change within the genus, but other genera of the same family may have a different chromosome number. Krause (1930) reports the haploid chromosome number in the species of *Dorstenia,* another genus of the Moraceae, to extend from 12 through 13, 14, 15, 16, 20, and up to 24.

In the 31 species of *Ficus* included in this investigation, 22 species have chromosomes very similar in shape and size, typical sets being those of *F. benjamina crassinervia* (fig. 1), and of *F. eugenioides* (fig. 2). These sets are also similar to chromosome sets of *F. carica* and *F. palmata* previously figured (Condit 1928). Seven of the 31 species have chromosome complements with at least two *U*-shaped or *V*-shaped individuals, while in two species, satellited chromosomes are present.

There appears to be little if any relationship between the chromosome morphology of these species and their taxonomic classification as given by King and others. These cytological studies, however, do help to emphasize specific relationships, as is later pointed out for three species of *Eusyce.* With the inclusion of more species cytological differences may have a greater taxonomic significance than is now apparent.

Judged by its wide distribution and the extreme complexity of its forms, the genus *Ficus* is probably of very ancient origin. The probable evolution of its closed receptacle or syconium from flat receptacles as found in *Dorstenia* or from the pear-shaped receptacle of *Trymatococcus* is discussed by Ridley (1930) and by Bernbeck (1932). Pollination of figs is accomplished by fig wasps (of several genera), the fruits of a particular species of *Ficus* being usually entered by a distinct species of wasp. Since various species of figs crowd one another in tropical forests it is not unreasonable to suppose, as suggested by Williams (1928), that hybridization takes place in nature. Pemberton (1921) shows that a species of *Pleistodontes,* whose regular host is *Ficus macrophylla,* also breeds successfully in the syconia of *F. columnaris,* although there is a question whether these two figs are specifically distinct.

Various theories have been advanced as to the phylogeny of the common fig, *Ficus carica,* among which is that of Trabut (1922) who believes it to be of hybrid origin. It is certainly true that in California the cultivated forms of *F. carica, F. pseudocarica,* and *F. palmata,* are interfertile and the syconia of all three species are inhabited by the same blastophaga. Cytological studies (Condit 1928) of these three species show that their chromosomes are the same in number and practically identical in morphological characters.

There is a phylogenetic analogy in the genera *Ficus* and *Rhododendron,* certain species of each genus having undoubtedly migrated from Asia to America by way of the land bridge which once existed. Sax (1930) shows that over a probable period of millions of years most of the species of *Rhododendron* have not undergone any change in chromosome number, and, more remarkable still, that the chromosomes of certain species have not changed fundamentally in their genetic constitution. In the American species of *Ficus* studied cytologically, namely *F. populnea brevifolia* and *F. mitrophora,* the chromosome complements are identical in number and morphology with those of various species from the eastern hemisphere. There appears to be no record of hybridization between any of the Old World species and the American species of *Ficus.*

In a recent paper Lawrence (1931) discusses the secondary association of chromosomes, i.e., a differential approximation of the bivalents in the equatorial plane, and its possible relation to the phylogeny of certain species. This secondary association is claimed to be of widespread occurrence in polyploids but is found only in plants with small chromosomes. From the secondary association found in the following genera, Lawrence draws the inference that they are secondary polyploids, viz.: *Salix,* n=19; *Gossypium,* n=13; *Xanthium,* n=18; *Ficus,* n=13; *Vitis,* n=19. He believes that the absence of low numbers in these and other genera and orders implies that the polyploid forms had a distinct advantage over the ancestral diploid forms, all of which are now extinct.

SUMMARY

1. This paper presents the results of a cytological study from root-tip preparations of 31 species of *Ficus.*

2. The diploid chromosome number in each of the 31 species is 26. In a single cell of *F. pumila minima* a tetraploid chromosome complement is reported and figured.

3. The chromosomes of 22 species are similar morphologically while the other 9 species appear to be characterized either by *U*-shaped, *V*-shaped, or satellited chromosomes.

4. A table is given showing chromosome numbers so far reported for 43 species of *Ficus.*

5. Chromosome morphology appears to have little significance in the taxonomic grouping of these fig species although it does have a bearing upon specific relationships of certain species, some of which may be of hybrid origin.

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CRITICAL NOTES ON
C. D. DARLINGTON'S
"RECENT ADVANCES IN CYTOLOGY"

BY

JOHN BELLING

(A posthumous paper)

WITH REPLY BY C. D. DARLINGTON

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CRITICAL NOTES ON
C. D. DARLINGTON'S
"RECENT ADVANCES IN CYTOLOGY"*

BY

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(A posthumous paper)

INTRODUCTION

To the student and to the researcher, this book may be of use, for here we have collected the chief results of the brilliant observational work done by the author and his collaborators during the last few years. The discoveries of other writers, which have a bearing (mainly a favorable bearing) on these results, have been diligently brought together as well, and these references and abstracts may also be found useful. The presentation of the material is, as we would expect, mostly at a higher intellectual level than the average with, however, occasional inexplicable lapses of memory or intelligence. Undoubtedly the volume would have been improved by a revision, after the author had received and considered the criticisms of other cytologists. Partly for the purpose of aiding in such a possible revision, but chiefly to afford students two opinions on moot points, and to correct obvious errors, I have written the following critical notes.

I am told that the book is found stimulating in university class work, perhaps too stimulating. My notes may help to bring the stimulation within bounds. The strongest points in the book are probably the observations of chiasmas and terminal junctions, in diploids and polyloids, at diaphase and metaphase. The weakest points seem to me to be the accounts of crossing-over, of chromomeres, and of living chromonemas.

The author's language is clear only if we bear in mind his peculiar use of common terms in different senses. In order to elucidate this (which, I am told, gives trouble to readers), I have introduced my own terminology, which has been prepared for use in a forthcoming paper.

The method of the author is to try to establish general propositions, and then to deduce from these. Unfortunately, to a general proposition there are sometimes enough exceptions to invalidate it. Thus the old "presence and absence" generalization has succumbed, after years of struggle, under the weight of the exceptions piled on it. The same fate has overtaken the generalization that crossing-over occurs only in definite ratios. The establisher of such general propositions tends to be somewhat impatient with the presenter of exceptions, as is seen in the author's treatment of Robertson's data. Hence, and for other reasons, his writing savors somewhat of propaganda, and the logic is sometimes unconvincing. It is unfortunate that the writer did not take as a model the impartial scientific exposition of *The Mechanism of Mendelian Heredity.*

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* This paper gives results of cytological work done under the auspices of the Carnegie Institution of Washington.

In my opinion, Mr. Darlington's book contains too many conjectures. A conjecture may be defined as a more or less plausible guess, stated and left, without work being done on it. No priority is due to such a bare conjecture, I think. If it is tested by all available relevant facts, and survives, it becomes a tested hypothesis. A tested hypothesis has some claim to priority. If the tested hypothesis is put to work in research for new facts, and succeeds in prediction, it becomes a theory, with strong right to priority.

Now if all cytologists printed all or most of their conjectures, the facts would be crowded out. Such literature would not be science. It is true that the discoverer of a new fact is allowed, I think, by general usage, a conjecture as to its origin. But the ratio of facts to conjectures should be kept in the ratio of food to wine. We know what happens when the wine is in excess. If the author would prune out nine-tenths of his conjectures in a second edition, his book would be far more reliable.

Suppose an examiner questions a graduate student in cytology; is he to be answered with a conjecture from this book? We must remember that students are less skeptical than more experienced workers, and may actually believe in the conjectures they see in print. If all the conjectures were marked with a "(C)", little harm would be done.

THE AUTHOR'S CHIEF DISCOVERIES

Since, in this book, conjectures are found close to accounts of new facts, I have sometimes found it difficult to distinguish between them. Such proximity of conjecture and fact is likely to cast doubt on newly discovered facts. Hence, it seems useful to list here the author's chief discoveries.

1. Some polyploids arose by doubling in the egg-cell line (*Rubus,* 1928).

2. The smallest chromosomes were found to have attachment constrictions (*Prunus,* 1928).

3. The chromonemas were found to synapse in two's at zygotene in some autotriploids (*Tulipa, Hyacinthus,* 1929).

4. The chromonemas were found to synapse in two's at zygotene in an autotetraploid (*Hyacinthus,* 1929).

5. Fragments of chromosomes were connected laterally (at metaphase) with whole chromosomes (*Tradescantia,* 1929).

6. Chromosomes after pachytene, at the first division of meiosis, were connected to form bivalents, either (1) by chiasmas, or (2) by terminal junctions which arose from chiasmas (*Tulipa, Hyacinthus, Fritillaria,* 1929, 1930).

7. The arrangement of the chromatids in pairs of adjacent chiasmas was traced, at anaphase in localized chiasmas, and also in triploids and tetraploids (1929, 1930).

8. Quadrivalents with non-terminal chiasmas had certain configurations explicable only by previous crossing-over (*Hyacinthus,* 1930).

9. In some plants the chiasmas were mainly near the spindle-attachment (fusal) constriction (*Fritillaria Meleagris,* 1930).

10. In different races of one species, genetic variation in frequency of chiasmas occurred (*Fritillaria imperialis,* 1930).

11. Single and multiple terminal junctions arose from the sliding of chiasmas to the ends of bivalents (*Primula, Campanula, Tulipa, Stenobothrus,* 1930, 1931, 1932).

12. Rings of chromosomes having non-terminal chiasmas were found, which were explicable by interchange (*Oenothera,* 1931).

13. The varying numbers of chiasmas in certain bivalents gave curves showing interference (1931).

14. A hybrid was found to have a lower number of chiasmas than either of its parents (*Triticum,* 1931).

15. The average numbers of chiasmas in certain bivalents were not proportional to the lengths (*Stenobothrus, Chorthippus, Hyacinthus amethystinus,* 1932).

16. The frequencies of formation of trivalents in some triploids, and of quadrivalents in certain tetraploids, were worked out, and a suitable hypothesis framed (1932).

17. Small chromosomes were found to have chiasmas which slid to the ends (1932).

18. Single chiasmas did not slide to the end, though a pair of chiasmas did (*Tulipa,* 1932).

TERMINOLOGY

In order, as noted above, to elucidate the author's terminology, I give here an interpretation of the terms as I use them.

"Allele"= allelomorph. I use "heterozygous" in the sense of "having one or more pairs of dissimilar alleles." On the other hand, "heterosomic" means "having a different gene arrangement in corresponding chromosomes."

"Partner" chromosomes are those that synapse (homologues).

"Sister" segments of chromatids are "conjunct" at earliest diplotene, before the chiasmas slide; after this, non-sister chromatids may have conjunct segments.

"Jugate" chromatids (which have usually crossed over) are connected at the "fusal" constriction.

The "fusal" chromomere seems to cause the attachment to the spindle, and also the attachment of the jugate chromatids to one another.

"Diplotene" is partly like pachytene, and ends with complete opening-out.

Early, middle and late "diaphase" last from diplotene to first metaphase.

"Chiasmas" are non-terminal.

"Junctions" are usually terminal.

DETAILED OBJECTIONS AND NOTES

Many of the following objections and notes are concerned with terminology, which is, I think, important for the new science of karyology. Some are expressions of opinion, but often two opinions may be preferable to only one. On some other points I differ from the author as to observations by myself or by others, or as to matters of fact or logic.

If the author of the book would consider some of the following notes and objections when preparing a second edition, the reliability of the volume, in my judgment, would be increased.

Chapter 1

p. 3, m.[*] "The products of cell division are usually dissimilar from the parent cell." They are more often similar to the parent cell, in my opinion. A review of the cytology of the chief plant and animal forms will, I think, show this. Such dissimilarity is shown indeed by cambium, but this only makes each year a (usually) thin sheet of wood and bast. Apical cells also give rise to different tissues; and unequal divisions are seen in megasporocytes, ovocytes, etc. Some groups of organisms show dissimilar divisions, such as diatoms. On the other hand, in perhaps most groups of one-celled forms, the products of cell division seem more often similar to parent and sister cells. In many-celled organisms, I think, the use of the word "tissue" usually assumes a majority of equal divisions.

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[*] Page numbers refer to Darlington's book, and the quotations are from that work. *t* = top third; *m* = middle third; and *b* = bottom third of page.

p. 5, t. "Fertilization" has long been applied, I think, first to the fusion of the two gametes (syngamy); and secondly (but not solely) to that of their nuclei (karyogamy). Thus Wilson says (1925, p. 394), "Fertilization comprises two closely associated but experimentally separable events." The author seems to use "fertilization" here as equaling "karyogamy."

p. 9, t-m. "Too little" .... "too much" nucleus, etc. I have found $n-1$ pollen grains, at the metaphase stage, in *Rhoeo* (unpublished), *Cypripedium* (1924), and *Uvularia* (1925).

p. 10, m. "Two embryos derived from" the embryo sac. This is strained language, I think. About half of the genes of the normal embryo come from the sperm; and the endosperm (with one-third of its genes from the sperm) is apparently not an embryo of anything, despite conjectures as to its origin.

p. 10, m. The normal embryo of flowering plants is, it seems to me, no more "a mere organ of the sporophyte" than a marsupial embryo is an organ of the female kangaroo.

p. 14, b. "Parasitic." A straining of language, I think; especially as applied to pollen grains.

Chapter 2

p. 16, b. "Chromosomes .... are of constant size." They may be much diminished by starvation (in new tissue) in plants (1927, MS).

p. 17, b. "Domestic analogy." This appears to me to be an unnecessary sneer at a plausible conjecture.

p. 17, b and 18, t. "The ends of the chromosomes stick to the nucleoli." This undervalues, I think, the proofs of the position on the nucleole of the satellited end of the bivalent at pachytene, and other stages (S. Navashin, 1927; Heitz, 1931; and McClintock, 1931); which I can also confirm.

p. 18, t. "Fragments of cytoplasm having no function." Surely a plain confession of ignorance would be better than this negative conjecture.

p. 19, t. "The substance expelled .... is more likely to be of nucleolar origin." This statement as to chromatin diminution in *Dytiscus* shows that the author seems to think that chromatin consists of genes. I consider that I have proved this latter conjecture to be erroneous (1928, 1931).

p. 19, m. "Mitosis" has usually included the longitudinal splitting of the chromonemas (see Wilson, 1925). The author's definition applies, I think, only to the anaphase of mitosis (cf. p. 89, fig. 18).

p. 19, b. "Double mitosis." In my opinion there is only one mitosis in the course of meiosis (cf. p. 88, t).

p. 20, t. "In living material the nucleus first appears granular." This is so, I think, only when good water-immersion objectives are not used. The normal, living, non-dividing nucleus shows coiled threads, in favorable objects (Martens, 1927, 1929; Belar, 1929; Belling, MS).

p. 20, b. "At the earliest stage .... the threads are double." I do not find this so in good smear preparations (MS), nor did Belar (1929 *b*).

p. 22, t. Discontinuity of chromomeres said to be exaggerated by fixation. The reverse is the fact, in my opinion (1928, 1931). With fixation below the optimum for smears, the chromomeres tend to run together.

p. 22, t. "Chromomeres .... artifacts." This is not so, in my judgment. The clearest chromomeres and chromioles are seen in pollen-mother-cells with walls slightly broken in smearing, so as to let in the fixative more quickly. By special destaining, I have demonstrated, at the cores of all chromomeres, in many cells of *Allium triquetrum,* bodies as sharply defined as centrioles (1931).

p. 22, m. "Indirect evidence." The proof of a spiral (or a spiroid) chromonema is sometimes direct, I think (Sakamura, 1927; Belar, 1929 *b*). I have seen the intermediate stages of spiral formation in *Rhoeo* (MS).

p. 24, m. "The 'fibers' that are seen are merely the channels between them." The 24 "traction" fibers of the spindle are real, I consider, in *Lilium.* I have, by starving, got them to show in a vacuole (MS).

p. 25, t. "Intercalary." This term is misapplied to the attachment point, I think; for it normally means "inserted among others," and there is only one attachment point. "Non-terminal" seems a better term.

p. 25, b. Half-chromosomes, at somatic metakinesis (Belar, 1929), or metaphase, first separating widely and then coming together again throughout their lengths. References to any other writers who have noted this procedure seem needed here.

p. 26, b. "A property correlated with the special distribution of its water content." Vague, as applied to the extension of the "stem-body" of Belar (1929).

p. 27, m. "Imbibition of water" at telophase. References to experiments for this are needed, I think—unless it is a conjecture.

p. 30, t. "A nucleus is a cell-body which arises or reproduces by mitosis." This ignores amitosis (*see* Wilson, 1925). A more inclusive definition might be, "A nucleus is the cell-body which contains the chromonemas or the chromomeres." This might include many of the Protista.

p. 30, m and *b.* By my measurements (1928, 1931), the leptotene threads in *Lilium* increase in length up to mid-pachytene. The contractions come later. The author says that this disagrees with the records in table 3. I am unable to find anything in the printed table which disagrees in this way.

p. 31, b. Chromomeres are, I think, the opposite of artifacts. The plain uniform string often seen at pachytene, in sections of material fixed in bulk is, in my opinion, the result of the chromomeres running together because of slow fixation.

p. 31, b. There is no proof, I think, that the spiral (or spiroid) is an artifact. It has been seen in living cells (Sakamura, 1927; Belar, 1929). A dictionary definition of artifact—with which I agree—is: "A structure or appearance in a tissue or cell due to death or the use of reagents, and not present during life."

p. 34, t. The primary constriction with its special chromomere (polar granule) can be seen at pachytene in *Agapanthus* (1928).

p. 34, b. "Ligature." This word seems used abnormally here. How is it better than constriction?

p. 35, t. With regard to the attachment chromomere, reference should be made, I consider, to Trankowsky (1930).

p. 38, t. "Intercalary" satellites. The author's bodies may not be true satellites, which rest on the nucleole in the prophases of mitosis and meiosis.

p. 40, b. The thick metaphase chromosomes are obviously not permanent structures; it is the chromonemas (gene-strings) in them which are permanent. The chromatin usually leaves the chromonemas, in the resting (non-dividing) stage.

p. 42, t. "The nucleus appears optically empty." But with Navashin's fixative and brazilin stain (using smears, not sections), the chromonemas can often be seen in resting nuclei (MS).

p. 42, m. "The threads branch and anastomose." The chromonemas, I think, only *seem* to branch (or become reticulate) in slowly fixed nuclei, such as those of sections of plant organs fixed *en masse* (MS).

p. 42, m. "To the eye of faith." This seems to mean that the chromonemas cannot be seen in sectioned material fixed in bulk, and stained with gentian violet.

p. 43, t. "Direct observations of structure in the resting nucleus have so far failed." Against this statement are the observations of Martens (1927, 1929), Belar (1929), and myself, with living nuclei; and those of Belar (1929) and of myself (MS) with resting nuclei in total or smear preparations, fixed and stained.

p. 47, m–b. "The evidence is valueless." Robertson's data (1931) are not easily waved aside. I think the matter requires more investigation by the proponents or opponents.

p. 47, b. "The permanent thread is .... double at prophase (except in meiosis)." References to observations are needed as to the doubleness of the chromonema in the earliest prophase of mitosis, if it is more than a conjecture. This does not show in smear preparations (Belar, 1929; Belling, MS).

p. 48, t. "During the resting stage .... longitudinal division." References are needed as to this division during the resting stage, unless it is a conjecture. It was not seen by Martens (1927, 1929), Belar (1929), or myself.

CHAPTER 3

p. 50, m. There seems no sufficient proof yet that the volume of the metaphase chromosome is proportional to the length of the contained chromonemas. References to measurements seem needed here, if this is not a conjecture.

p. 50, b. There seems no sufficient proof yet that the diameter of the metaphase chromosome is proportional to the contraction of the contained chromonemas. My experience leads me to disagree with the statement. References to measurements are needed, if it is not a conjecture.

p. 50, b. The length of the first metaphase chromosome is, in my opinion, not proved to be proportional to the length of the pachytene chromonemas, nor to the amount of their contraction. I find that new chromatin is added (1928, 1931). References to measurements are needed, if there are any.

p. 53, m–b. "Changes in bulk .... ascribed to differences in dispersion of the .... genes." References are needed here, unless it is a conjecture.

That size differences of metaphase chromosomes may be due to more or less chromatin, and not to the arrangement of genes, I consider I have proved in *Lilium* (1928, 1931).

p. 61, t. This basic x is sometimes conjectural, as in Langlet (1932).

p. 62, t. "Reunion, after separation, of nuclei." References are needed, I think. This seems to require more observational proof as a "chief occasion of polyploidy."

p. 66, b. "Failure of pairing." This apparently means here, "asynapsis" or "non-conjunction."

p. 67, b. (v). Deficiency or deletion following fragmentation. In my theory of crossing-over, these do not follow fragmentation, but follow rearrangement at an overlap during division of the chromomeres.

p. 70, m. "Reduplication" = duplication (Bridges).

p. 73, t. "Structural change." Few changes in chromosomes are not structural, I think. Thus, mutational changes in the individual genes and changes of mere chromatin being excluded, we have left the "gene rearrangement" of Muller, which I call "heterosomy."

p. 73, m. There is not sufficient proof, in my opinion, to show that chromosome segments without a spindle-fiber-attachment chromomere (fusal chromomere), can form or borrow a new one. References to observations are needed here, unless it is a conjecture.

p. 73, b. "Fusion only occurs between .... fragments." In my theory of crossing-over and interchange, there need be no breakage or fragments in translocation.

p. 75, t. Possibly some of these fragments had no fusal chromomere. This requires proof in each case.

p. 76, m. It seems to me to need more observational evidence to show that constrictions arise at the true points of crossing-over or of interchange.

p. 80, t. This comparison of species, where two rod chromosomes seem to replace one *V* chromosome, was displayed excellently by Metz in *Drosophila* species, in 1914 and 1916.

p. 85, table 12. It is not clear to all readers whether these breadths and lengths are (1) averages of the complement, or (2) maxima of the complement. They are in fact maxima.

Chapter 4

p. 88, t. Definition of meiosis as "Two divisions of a nucleus accompanied by one division of its chromosomes." This omits synapsis (conjugation) of chromonemas; an essential stage of meiosis, in my opinion. The author's definition would agree with the phenomena in pollen-mother-cells of a haploid Datura; which is not a model for meiosis, in my opinion.

p. 90, t. The leptotene threads "come into contact at various points at random." More observational evidence as to this seems wanted. Some leptotene threads certainly start synapsing at the distal ends near the antipole.

p. 90, t. "The double or bivalent threads contract further" at pachytene. In *Lilium, Fritillaria,* and probably in some other organisms, there is a growth in length after early pachytene (1928, 1931).

p. 90, t. "Signs may appear of the thread being quadruple." The secondary split starts at mid-pachytene, in *Lilium* (1931).

p. 91, t. "Later stages have a purely mitotic character." Not in *Datura, Cypripedium,* and other plants, where the second metaphase chromosomes differ from those in the metaphase of mitosis, as the author notes later on.

p. 91, m. I object to the use of the word "pairing" for (1) synaptic conjugation of homologous (partner) chromosomes, (2) closeness of conjunct sister segments of chromonemas at internodes, (3) connection of jugate chromatids at the fusal chromomere, (4) closeness of conjunct non-sister segments of chromatids at internodes, after sliding of the X of a chiasma, (5) union by chiasmas, (6) union by terminal junctions, (7) approximation during first metaphase, (8) approximation during second metaphase, and (9) approximation during the metaphase of mitosis. "Pairing" might well be used for the last three; and synapsis, conjunction, jugation, terminal junction, chiasmal junction, etc., used for the others.

p. 92, t–m. "If they are polarized they usually associate first at their attachment constrictions, whether these are median or terminal (Wenrich, 1916, 1917)." Synapsis does not usually commence at the attachment constrictions, but apparently often at the distal ends of the chromonemas, which in polarized leptotenes are at the antipole (Janssens, 1924; Schreiner, 1906; Robertson, 1916; Mohr, 1916; Gelei, 1921; Belling in *Rhoeo,* MS, etc.). Wenrich's contrary speculation as to the

V chromosomes of *Chorthippus* and *Trimerotropis* seems unconfirmed, even by his own figures of zygotene.

p. 93, b. "During pairing [synapsis] the chromosome threads contract linearly." They do not do so in my preparations of diploid *Lilium* (1928) and *Allium* (1931). I also fail to see evidence for this in some published figures of the zygotene of diploids.

p. 94, t. "Wenrich was able to represent each of the paired chromosomes." Wenrich dealt here, in my opinion, with compound chromomeres at diaphase. He had previously pictured the ultimate chromomeres of true pachytene (1916).

p. 94, t. "The chromosomes were already contracted." The stage was early or middle diaphase, I think.

p. 95, t. True diplotene (E. B. Wilson, 1925) resembles pachytene nearly as much as it resembles diaphase. The author calls early diaphase, and sometimes middle diaphase, "diplotene."

p. 95, t. "The pairs change partners." Apparently a "pair" here consists of the members of one side of an internodal segment; while "partners" are any two jugate chromatids connected at the fusal constriction. I do not care to use "pair" in this sense; and would like to confine the word "partner" to non-sister synapsed chromosomes, chromatids, segments of chromonemas, or chromomeres. (Cf. *p. 91, m.*)

p. 95, b. "The mean number of chiasmas per bivalent is approximately proportional to the length of the paired chromosomes." What is "approximate?" Is 5 per cent of error the limit, or 25 per cent?

p. 98, t. Accurate proportionality would give 8.4 chiasmas in the third column, instead of 6.2; an error of 26 per cent.

p. 98, t. "It seems to be at random with regard to the different parts of the chromosome—whether proximal or distal." The distribution of the chiasmas at pachytene, diplotene, and early diaphase is, in my opinion, not necessarily at random with regard to the ends or the attachment constrictions of the chromosomes. There is interference in some cases.

p. 100, t. "The chiasmas formed at diplotene." They are formed at pachytene (Belling, 1931; McClintock, 1931).

p. 100, m. "Until diakinesis." This omits early and middle diaphase (see E. B. Wilson, 1925).

p. 103, t. "The connection is not between two whole chromosomes." It more often appears to be so. Single junctions are common in my observations.

p. 103, t. "Association." The author uses this word sometimes as equivalent to "pairing," and in almost as many senses; with similar resulting confusion.

p. 103, t. If a chiasma, formed at late pachytene, is defined as two diagonals making an X, and two new longitudinal connections (crossovers); then a true terminal chiasma is a contradiction. It seems to me that at the end of the bivalent the sliding X of the chiasma either slides off, or facilitates a terminal junction between the distal chromomeres.

p. 104, t. "As though it had a single attachment." It perhaps has a single attachment chromomere in *Agapanthus*.

p. 104, t. "The two attachments .... repel one another." References to experimental or observational proofs of this repulsion are needed; otherwise it remains a conjecture.

p. 113, t. "Compensating chiasmas." I find, at pachytene, two kinds of single chiasmas, direct and oblique, in about equal numbers. There are two directions of overlap. Hence, on my theory of crossing-over, there are sixteen different kinds of double chiasma. These may be reduced to eight, for most purposes. Of these eight, two (similar supplemental pairs) give two double crossovers and two non-crossovers; and two (similar complemental pairs) give four single crossovers. These four similar pairs are the author's "compensating" pairs. The other four pairs of chiasmas are "unlike" (one oblique and one direct), and give one double and two single crossovers, and one non-crossover. These unlike pairs are the author's "non-compensating" pairs.

p. 113, t. "Association of chromatids." This is vague. "Longitudinal sequence of jugate chromatid parts," is apparently meant.

p. 114, top line. "Prophase" should apparently be "interphase."

p. 114, t. "Associated chromatids." Jugate chromatids, held together at the fusal constriction, apparently.

p. 114, t. "Association with other chromatids." Either conjunct segments of sister chromatids before sliding of chiasmas, or conjunct segments of non-sister chromatids after sliding of chiasmas.

p. 114, b. "In a triploid .... one thread is left out of association." This is at zygotene. I found also, in 1929, some conjunct triple threads in *Hyacinthus,* later than zygotene. I am reinvestigating the matter using fresh material of *Hyacinthus, Tulipa,* and *Lilium,* and with the advantage of improved methods.

p. 116, t. "The number of changes of partner is limited." "Change of partner" in the author's language, seems to mean in triploids the presence of either (1) a recurrent or (2) a progressive chiasma, or (3) a partial progressive synapsis. Here it apparently means the last. The number of changes cannot be inferred from the numbers of chiasmas; and they cannot, in my opinion, be readily counted at zygotene, in *Tulipa* or *Hyacinthus.*

p. 116, t. "Is largely influenced in its choice of partner." Proof is required that it has any choice, and that it does not synapse with the nearest unsynapsed homologous chromomere.

p. 118, b, and 120, t. "In several triploids.... the chromosomes have been said to associate fully, i. e., in *x* trivalents.... (e.g. *Canna,* Belling, 1921; *Datura,* Belling, 1927;.... *Hyacinthus,* Belling, 1928)." With regard to me this is surely wrong. I wrote, in 1921, about a triploid Canna (Proc. Nat. Acad. Sci., **7**:197–201): "In several prophases, one chromosome was disconnected from its corresponding dyad." I wrote in 1923, about triploid Daturas (Proc. Nat. Acad. Sci., **9**:106–111): "Occasionally one (or more) of the single chromosomes or chromosome pairs remains isolated." Also with regard to tetraploid Daturas: "Sometimes one or more pairs, or single chromosomes remain unconnected." I wrote in 1927 (Jour. Genetics, **18**:177–205, p. 186): "Hence, also, arises the frequency of separate single chromosomes (univalents) in the triploids, as compared with the diploids, where they are rare. In the true triploid Cannas, for instance, almost every other pollen-mother-cell may sometimes show one or two separate univalents." On page 188, referring to the uneven distribution of chromosomes in tetraploid Daturas, I wrote: "This is probably due to the fairly numerous cases of separation (non-conjunction) of chromosomes. It is, in fact, difficult to find a tetraploid group without some separate chromosomes." There is no particular credit due to the first observer of this (who was probably Osawa, in 1920); for the matter *saute aux yeux* in any well fixed preparation of pollen-mother-cells.

p. 121, m. "Chromosomes.... held together." The chromosomes of bivalents are not always held together only by chiasmas at metaphase. There are often terminal junctions, which I do not call chiasmas because they do not agree with my definition of a cytological chiasma as "a decussation at an overlap with crossing-over in two chromonemas."

p. 122, t. In the triploid Drosophila, interference of crossovers is apparently reduced (Bridges and Anderson, 1925; Redfield, 1930, 1932). Why should not interference of chiasmas also be reduced in the triploid hyacinth?

p. 123. Figure 35. These figures, in my judgment, are diagrammatic, and should be so described.

p. 125. Description of figure 36. "Something has not yet divided." This may be the fusal (or attachment) chromomere seen in *Agapanthus* (1928).

p. 127, m. The word "paired," in the author's usage, has engulfed the more definite words: *synapsed* or *conjugated; approximated; united; fused; conjunct;* and *jugate.* (Cf. *p. 91, m.*)

p. 127, m. "Pairing between diplotene and metaphase is only between pairs of chromatids." Between [segments of] members of pairs of chromatids, is meant. However, these [segments of] members of pairs are usually zigzag or spiral, and are held together by extra chromatin (1931).

CHAPTER 5

p. 129, t. Definition of heterozygote. A more up-to-date definition of a heterozygote might perhaps be, "an organism with one or more pairs of genes formed of different alleles." But a heterosomic organism has different gene arrangements in corresponding chromonemas. And a true hybrid organism might perhaps be defined as coming directly from either a varietal cross or a species cross.

p. 129, m. "Hybrids have very generally the property of hybrid vigor or heterosis." If "hybrid" here = "heterozygote," then a large number of organisms heterozygous for a few alleles show no hybrid vigor, but the reverse; as is seen in the hundreds of heterozygous Drosophilas. Simple heterosomic organisms also normally show no hybrid vigor. It is obvious that "hybrid" here is used in the sense (not intended in the author's definition) of varietal or species cross, usually for the first filial generation only.

p. 129, b. "The heterozygous sex in an animal hybrid is not strictly an F_1 hybrid . . . ., since it differs from the hybrid of the homozygous sex through the hybridity of one of its parents." "Animal hybrid" is apparently used here in the sense of varietal or species cross, for the two X's (or two W's) are supposed to be heterozygous. "Heterozygous" in the beginning, and "hybridity" near the end, have apparently the same sense, namely, the heterosomic state of the X (or the W) chromosome in one sex.

If, as the author assumes, "hybrid" means the same as "heterozygous," then we may rewrite the above quotation as, "The heterozygous sex in an animal heterozygote is not strictly an F_1 heterozygote . . . ., since it differs from the heterozygote of the homozygous sex through the heterozygosity of one of its parents." The meaning, I think, is not clear.

p. 130, t. I do not agree that an autotriploid should be called "hybrid" without knowledge of its derivation from a cross.

p. 131, b. "Mendelian differences for the cytologist are those which have no recognizable effect on chromosome behavior." Some Mendelian differences have an effect on chromosome behavior. Such are the allelic differences which determine asynapsis (Beadle, 1930; Gowen, 1928), and long or short first metaphase chromosomes (Lesley and Frost, 1927). Also (and more pertinent) since the chromomere is the constituent unit of the chromosome, and synapsed chromomeres may show size differences, absence, or doubling, it seems that Mendelian differences do affect *chromomere* behavior.

p. 132, t. "Many large differences, as in triploidy, which are incapable of Mendelian analysis." This seems doubtful to me, recalling the excellent Mendelian work already done on triploids by Blakeslee, 1923); Bridges and Anderson (1925); and Redfield (1930, 1932).

p. 132, m–b. "Lateral chiasma." More observational proof seems to me to be needed to show that the lateral junctions represented in figure 39 were caused by chiasmas.

p. 136, t. "This is due to the fragment usually, ..." The two explanations proposed are not certain, and another is possible.

p. 136, t. "Where the fragment corresponds, ..." This seems circular reasoning, to me.

p. 136, m. "This failure is expected, ..." This may be so, or may not be so, in my opinion.

*p. 137, t, table 17.*This is not made clear, nor is its relevancy stated.

p. 137, b, table 18. In *Matthiola,* the calculated frequency is about 70 to 100 per cent wrong (as the author himself states).

p. 139, t. "Secondary trisomics." There is omitted here the fact that the phenotype of any particular secondary trisomic Datura was the same in different occurrences of the mutation.

p. 143, b. "The point of interchange is in the neighborhood of the spindle attachment." This is not the case in McClintock's well proved case in *Zea* (1930); nor in Cooper and Brink's well studied case of another interchange in *Zea* (1931).

CHAPTER 6

p. 156, m. "Identical chromosomes." This is, I consider, not an improvement on the old term, "homologous chromosomes." Presumably sister chromatids at mitosis may be regarded as identical; but not the homologues of meiosis, nor the jugate chromatids which have usually crossed over.

p. 156, m. "In triploids .... at random." There still seems to be some interference among recurrent, if not among progressive chiasmas.

p. 156, m–b. "Pairing is therefore not a property of the chromosome as a whole, but of its constituent parts." This was finally proved by Gelei in 1921, I think.

p. 159, t. "Differentiation in the chromatin material." The author again supposes, apparently, that the genes are chromatin.

p. 159, m. "Only identical genes may pair." It is probable that I have also seen some alleles synapse, when differently sized partner chromomeres met and were connected by a cross-thread.

p. 159, b. "Pairing in different hybrids." Metaphase union is apparently meant here.

p. 161, t. "Assumption that .... a larger or smaller fraction .... is paired at pachytene." This requires proof by observation of the pachytene, I think. (See McClintock, 1931.)

p. 165, b–166, t. "Unpaired chromosomes .... divide." They do not do so normally in my observation of $n + 1$ Daturas.

p. 168, m. "Univalents .... able to divide." Univalents do not normally divide at the first division in n, $2n + 1$, $2n - 1$, $3n$, $3n - 1$, $4n$, $4n + 1$, and $4n - 1$ Daturas, in my experience.

CHAPTER 7

p. 169, t–m. Quotation from Bateson, 1922. In 1914, I sent to Bateson, who had previously made a similar remark, an account of indubitable semi-sterile plants arising from completely fertile parents, under accurately controlled experimental surroundings. (Crosses between certain fertile F_1 plants would fulfill his conditions.) His repetition of the above statement, eight years after, was obviously due to forgetfulness.

p. 169, m. "Set" here is what I called a "group," in my first studies of triploids in 1921. I said, "We may define a triploid plant, in the strict sense, as one having a chromosome group made up of a number of sets of three homologous chromosomes." My use of the term "group" is the same as that of E. B. Wilson (1925, p. 870).

p. 169, b. "It may be derived immediately." It rarely is, apparently.

p. 170, m. "At the extreme in the other direction is *Raphanus-Brassica.*" Extreme allotetraploids, such as this (Clausen and Goodspeed, 1925), are perhaps better called amphidiploids.

p. 179, t. "Inverse correlation." In a loose sense only, not in the accurate use of the term.

p. 181, b. "Gametic doubling.... does occur more freely in haploids and in hybrids." Does it? I have found large percentages of it in pure diploids (MS).

p. 183, b. "Autosyndesis." "Autosynapsis" seems the preferable term, since we have the verb "to synapse" (Bridges).

CHAPTER 8

p. 219, t–b. "The daughter chromosomes have remained together." This was well shown in the double pollen grains of *Uvularia* (1925), and of *Gagea* (Sakamura and Stow, 1926).

CHAPTER 9

p. 228, b. "The existence of qualitative differences between genes in the same complement is evidence of gene mutation." But we do not know how the genes at different loci arose. The evidence of gene mutation at any one locus by x-rays is direct. But this mutation is usually more or less quantitative.

p. 229, b. "Qualitative differentiation of the chromosomes." This means "differences observed." We know little about the process of differentiation.

p. 230, t. Gelei (1921) observed the synapsing of pairs of ultimate chromomeres distinguishable from other pairs by their size. The author of this book apparently did not observe independent pairing in "blocks" one chromomere long.

p. 231, t. I have seen $n-1$ pollen grains at metaphase in *Rhoeo* (5 chromosomes) and in *Cypripedium* (9 chromosomes), as already stated.

p. 231, m. "The zygote of a plant or animal can never develop when lacking either a section or a whole chromosome of one type entirely, i.e. in both sets." The smallest section is one chromomere. It has not been proved that no viable recessives are absences, as this statement would require. It has also not been proved that all homosomic deficiencies are lethal.

p. 231, m–232, t. Definition of haploid complement. This definition seems to me not to fit. It assumes that no viable recessives are absences. It also assumes that all homosomic deficiencies are lethal, and that no inactivated genes are present.

p. 231, table 38. The author might have quoted my second-metaphase counts in triploid Daturas (1922), which are more reliable than the pollen-grain counts of *Hyacinthus* (1924), because of a recorded source of error in the latter.

p. 235 (last word). "Super-male" should be super-female.

p. 237, m. "Every integral part of the chromosome complement is necessary for the normal development of every part of the organism." The first "every" can be disproved if some viable recessives are absences or inactivations. The second "every" I consider erroneous, since many or most homozygous recessives only affect certain characteristics. If "integral" means "necessary," the statement is meaningless.

p. 237, b. There seems no apparent reason why the genes should only interact in two's, and not in three's, four's, etc. "Interact" usually means "to act upon one another" and not "to act together." "Proportions" does not mean "interactions" in the first of these two senses.

p. 237, b. Apparently, on the author's basis, n should be $n - 1$ in the last line but one, since a gene does not presumably react with its duplicate.

p. 238, t. The least unbalance, in my opinion, should be when the whole of the chromosome complement n is doubled, giving $2n$.

p. 238, t. "The rule applies to *Drosophila.*" I cannot agree that this is proved. It might be that it is one-third and not one-half that gives most unbalance in *Drosophila,* for all we know. The rule can not be arithmetically valid, I think, since the genes are of different potencies.

p. 239, m. "Natural selection consists in the elimination of unbalanced forms." It consists in more, I consider, unless every point mutation is styled "unbalance"; which was not Bridges' or Muller's use of the term.

p. 241, t. If there is any slight synapsis in haploids, which I doubt for *Datura,* it can better be proved at zygotene and pachytene, than by approximations at metaphase.

p. 242, t–m. "Fragments .... probably due to crossing-over .... at non-corresponding positions." This requires proof, or else it remains a conjecture.

p. 242, b. "Illegitimate crossing-over." If the segments that cross over are presumed to be homologous, why call the crossing-over "illegitimate"? Crossing-over between non-homologues seems better called "illegitimate."

p. 243, m. "Reduplication of genes." Duplication of genes is conjectural, in my opinion, in homosomic normal forms, except in the bar locus (Sturtevant 1925, 1928). Translocations leading to duplications in the progeny seem rare and seldom to survive.

p. 243, m. "Haploid sets will probably contain a proportion, perhaps a majority, of their genes represented two, three or more times." This seems intended to refer to organisms outside the Oenotheras, etc., i.e., to homosomics. But genetics does not show it to be true. For if *Aa* and *Aa* occurred by point mutations in different loci in a diploid there would be regular 15 to 1 ratios. These are rare or absent in simple diploids. Interchange which survives is rare in nature (except in the *Oenothera* type of balanced-lethal heterosomics), as Blakeslee has shown in *Datura*. Heterosomics are usually partly sterile. A perhaps more promising way of duplicating single genes is unequal crossing-over (Sturtevant).

p. 244, t. "Reduplicated at one stroke with polyploidy." This could not well happen in animals (see Muller, 1925).

p. 244, m–b. The ultimate chromomere is the unit of crossing-over. The gene can then be identified as the core of the chromomere. It is thus not theoretical, but actual.

p. 245, t. "Specificity in pairing properties is usually inferred from observation .... of meiosis in hybrids." It should be gathered directly from observations at pachytene (cf. McClintock, 1931; Beadle, 1932).

p. 245, m. "The different genes making up one genotype .... must be qualitatively and not merely quantitatively distinct." They may be possibly (1) quantitatively active, (2) qualitatively active, (3) both quantitatively and qualitatively active, (4) neither quantitatively nor qualitatively distinct, but inactivated.

p. 245, b. "Qualitative, i.e., intragenic change." This is usually *quantitative* in its *effect*, in my opinion (cf. most mutations in *Drosophila*).

p. 245, b. Since Sturtevant's discovery of a cause of increase of genes in unequal crossing-over, it has been probable that some mutations are caused in this way; and that such duplication of genes may be important in species making.

p. 246, m. "All distinctions between genes .... arise from the same kind of intragenic change." This is probably wrong; for the two are different. Point mutations are *usually* quantitative in their effects; genes at different loci are *often* qualitatively different.

p. 246, b. "Intragenic change will prevent pairing of two genes." This is doubtful, for I have seen chromomeres of different sizes synapsed, and connected by a cross-thread.

p. 246, b. "Quantitative change will prevent pairing." Quantitative change, in the author's sense here, by multiplication of a gene, has not yet been proved except in one case (at the bar locus). "Structural change" is usually rearrangement in homosomics, and heterosomics do not usually survive apparently in competition with homosomics.

p. 246, b. "Allelomorphism is a function of position in the chromosome." This is a dubious conjecture. Alleles at the same locus usually produce more or less of the same effect. Genes at different loci usually differ qualitatively in their effects.

p. 249, top line. Should refer apparently to Gregory and to Blakeslee also.

CHAPTER 10

p. 252, b. "Reduction in number does not occur at either division." This depends on the definitions of a chromatid and a chromosome.

p. 253, t. "The classical theory." In my opinion, Janssens' theory alone deserves to be called classical.

p. 253, b. "All points at which four chromatids come together are points at which the pairs of chromatids exchange partners." This seems not fully proved (see Belling, 1931, and McClintock, 1931).

p. 254, diagram, B_1 and B_2. In both these, some of the diagonals of the X are crossovers. This does not occur in my theory of crossing-over, where the diagonals are non-crossovers at a chiasma.

p. 256, t. A chiasma always (in my experience) presents a St. Andrew's cross when it arises at pachytene.

p. 256, t. "Exchange of partner." Before crossing-over (at early pachytene) there is one pair of partners (homologues). After crossing-over (late pachytene and diplotene), there are two pairs of attached (jugate) chromatids. At early diaphase two jugate chromatids may be conjunct in the internode on one side of a chiasma, and separate on the other side. This is the author's "exchange of partner."

p. 257, b. "Equational chiasma." These are apparently diagonal, and could not normally come from opening out, in my opinion.

p. 259, figure 69. Here again the chromatids forming the X are crossovers, which does not agree with my theory.

p. 260, t. "The assumption that all apparent points of contact between four chromatids at diplotene are exchanges of partner." *See,* against this, McClintock's extra nodes at pachytene (MS), and my counts of extra nodes in *Lilium* from early diaphase to metaphase (1931).

p. 263, t. "An interchange and reduplication heterozygote." A heterosomic plant. There was perhaps no necessity to assume duplication. The terminal knob (the author's extra segment) was possibly an allele of the smaller terminal chromomere in the knobless strain.

p. 265, t. "Sister chromosomes are united." "Remain conjunct" (side by side) before the chiasma has slid, is meant.

p. 265, b. "Remote possibility that all three chromosomes in a triploid might conjugate successively (in time) at pachytene." On p. 116, t, and p. 266 (footnote), the author denies this.

p. 265, b. "This is inconceivable in a tetraploid." I can imagine it in detail.

p. 270, t. "Constriction .... at the position of a chiasma." But the chiasma is usually supposed to have slid before anaphase, and then the constriction will not mark the actual position of crossing-over.

p. 273, b. An interchange (reciprocal translocation), at meiosis, might make a figure of 8, with a "chiasma" at the joining.

p. 276, t. "Wenrich's unequal chromosome pair C_1 has a median spindle attachment." This can also be explained by the occurrence of one or two chiasmas, with a subterminal or terminal fusal attachment.

p. 277, m. "A single chiasma must *always* be formed." This requires proof. There may be terminal junctions. There may be occasionally no chiasmas and no crossovers. If this is excluded by "where pairing is by chiasmas," the statement seems meaningless.

p. 278, t. If there is 50 per cent of crossing-over at a localized point in the fourth chromosome of Drosophila, then the mutants already found in it are presumably at loci on the same side of this point; which does not seem probable.

p. 278, m. "Random." Recurrent crossovers are equal to progressive crossovers (Bridges and Anderson, 1925; Redfield, 1930). However, the positions are not necessarily random.

p. 278, m. "Non-hybrid triploids." The author has already classed all triploids as "hybrids" (see p. 130).

p. 279, t. This account of Anderson's attached X's does not state the fact that the two attached X's normally remain attached, and segregate as one chromosome (Anderson, 1925, 1931).

p. 279, m. "Factors situated more than 50 units away from the spindle attachment should be freely assorted." There seems to be a confusion here. If uncorrected crossing-over percentage (recombination) is meant, there can be nothing above 50 per cent, according to my theory of crossing over. If corrected crossing-over chart distance is meant, the statement is not necessarily valid.

p. 279, b. "More than 1/6 of homozygotes appear." The assumption of 1/6 in attached X's seems not to fit the facts, and also requires sister-strand crossing-over. These homozygotes equal nearly 1/2 of the percentage of (single plus triple, omitting most double) crossing-over to their right, giving nearly 25 per cent as maximum, in attached X's.

p. 279, b. "Random segregation of chromatids." In Anderson's attached-X case, homozygosity of heterozygous alleles is made by oblique chiasmas, not by direct chiasmas. This gives only ¼ homozygotes, with nearly ½ of 50 uncorrected units (25 per cent) as maximum.

p. 280, t. "Maximum crossing-over distance of 50 units." This usually includes much double crossing-over, and often some triple. "Units" here must mean uncorrected percentages, not chart units.

p. 280, b. There is another explanation of this, depending on the starting point of synapsis.

p. 281, b. Branching was not proved by the microscope.

p. 284, t–b. "The male character of localization of chiasmas inhibited, ... " This seems a complicated conjecture.

p. 285, m. "The distribution in position in the chromosome of chiasmas may be random . . . . although their distribution . . . . in relation to one another is not so." I do not agree with this. If the position of the chiasmas is truly random, there is then no interference, I consider.

p. 285, b. The method of measuring the internodes at (true) early diaphase is a fair one, in my opinion, in cases like that of *Lilium,* where there is little sliding of the chiasmas. Workers on *Zea* will perhaps soon be measuring internodes in maize pachytene. In calculating random chiasma formation for the *M* chromosome of *Vicia faba,* from Maeda's data, good results will perhaps be had by considering the probable number of chromomeres between which chiasmas can appear. The total number would probably not differ much from that found in *Lilium.* In this way the standard deviation can be shown to be much greater for chance formation of chiasmas than for the actual numbers (Haldane, 1931, and also S. Wright, *in litt.*).

p. 286, t. "Little is known of the frequency." I have found, from Anderson's data on attached X's (1925), the frequencies of direct and oblique proximal chiasmas; and they were nearly equal (30 to 30.3).

p. 286, m. "Function." This seems to me loose usage of an exact term. As shown above, there may be 26 per cent of error.

p. 288, b. "The question of how crossing-over comes to take place is necessarily much more speculative." This depends on what is seen at pachytene. I have seen both direct and oblique chiasmas at pachytene. The author considers only early diaphase.

p. 289, m. "The torsion is not lengthwise like that . . . . in the earlier expositions." The bending at an overlap is apparently mainly lengthwise.

p. 289, b. "Precocity theory." This conjecture relates to what happened during Archaeozoic times, and hence appears to be difficult to confirm.

p. 289, b. "At the moment." My observations show that it is not "at the moment," but just after.

p. 289–290. (Referring to chromioles not being longitudinally united at first.) This is no assumption of mine. I have seen it.

p. 290, t. "Crossing-over at the end of pachytene." Crossing-over occurs before the end of pachytene.

p. 290, t. "Coincides with the beginning of the assumption of a spiral." Again the author omits true diplotene, which has no spiral. It is in early diaphase that the spirals normally begin.

p. 290, b. "If the spiral arises in this way it should turn in the opposite direction on the two sides of the spindle attachment." According to Nebel (1932) it does not always do so, there being sometimes about 50 per cent of variation.

p. 291, t. "This structure is difficult to understand in terms of the properties of the genes." It is better demonstrated the better the fixation. I fail to see the difficulty of each gene's having a chromatin coat of specific thickness, as has been demonstrated (1931).

p. 291, t. "Pellicle." Apparently undemonstrated.

p. 291, b. "The property of differential precocity .... can scarcely be developed, ..." It may be due to one gene, or more, like many other properties of single chromosomes.

p. 292, m. "Although the length of the chromosome paired is reduced." My observations do not quite agree.

p. 292, m. "In *Drosophila* crossing-over seems to be concentrated, ..." This is perhaps because the first internode starts from one particular end of the chromosome.

p. 292, b. "Indicate a common control." This is not proved.

p. 293, t. "Chiasmas result from crossing over between two chromatids of homologous chromosomes." Chiasmas, by my theory, may occur also between non-homologous chromosomes in interchanges.

CHAPTER 11

p. 294, t. "Prediction." By Weismann, is meant.

p. 295, t. Three reasons are given, but another reason is perhaps that the ends at pachytene are sometimes not free (*Lilium, Agapanthus, Aloe,* etc.) but join laterally on to other chromonemas.

p. 296, m. "Homology .... can be tested in the chromosomes by their pairing properties." This is best done at pachytene.

p. 296, b. "This conclusion .... is equally clear from the observations of McClung and Seiler." Why then did no one reach it? Apparently it was not "equally clear."

p. 296, b. "Very small segments." Gelei (1921).

p. 299, t. "All association of chromosomes after pachytene is essentially of this kind." This has not yet been proved to be without exception.

p. 299, b. "Meiosis has always been recognized as a form .... of mitosis." Since they may have differed in Archaeozoic times, this statement is difficult to test by experiment or observation.

p. 299, b. "The immediate problem of meiosis is .... how it is related to mitosis and how it can have been derived from it." This "problem" is, in my opinion, unscientific. For meiosis consists of one mitosis plus synapsis (conjugation) of chromomeres, plus crossing-over, plus separation of partners (homologues). Synapsis, crossing-over, and separation of partners must (on the theory of the gene) be due to genes, which doubtless arose before Graptolites and Trilobites; and hence do not concern us, experimentally, so much as more tangible problems.

p. 300, b. "The chromatids are attracted to one another in pairs during prophase" of mitosis. This seems a conjecture. References to observations are needed, if it is not.

p. 301, m. "Which resembles structurally the double thread at the prophase of mitosis." "Structurally," i.e., in nature of alleles and arrangement of genes, the two synapsed threads at early pachytene may differ from the two identical threads in mitosis, in many ways of heterozygosis and heterosomy.

p. 302, t. "The thread must divide." If the author means by "thread" the fibers joining the chromomeres, my observations show that they do not divide. New supplementary fibers arise in an equal number.

p. 305, b. "Perhaps all nuclear division, apart from the first division of meiosis, is determined by division of the chromosomes." In this case, which is however unproved, division of chromonemas would seem to be the first stage of mitosis; and would not, as the author assumes, occur during the resting stage.

p. 307, m. The essential part of meiosis, in my opinion, is synapsis (conjugation), which has not been proved to occur in mitosis.

p. 307, b. "Meiosis differs from mitosis in the nucleus entering prophase before the chromosomes divide instead of after they divide." I do not agree with this, regarding it as unproved. Martens, Belar, and myself have made contrary observations.

p. 307, b. "Meiosis must have arisen at a single step." This is a conjecture, and possibly wrong. The origin of meiosis goes back many million years, and so is difficult to prove experimentally or by observation.

CHAPTER 12

p. 309, m. "An association in which the effective unit is not the chromosome but the chromatid." In zygotene it is chromomeres and chromosomes, not chromatids, which attract and synapse.

p. 309, b. "An interstitial chiasma is always of one kind." I think that all chiasmas are non-terminal, and that chiasmas may be of two (or four) kinds, namely, two direct, with crossovers $\genfrac{}{}{0pt}{}{(a+b)}{(b+a)}$ or $\genfrac{}{}{0pt}{}{(a'+b')}{(b'+a')}$ and two oblique, with crossovers $\genfrac{}{}{0pt}{}{(a+b')}{(b'+a)}$ or $\genfrac{}{}{0pt}{}{(a'+b)}{(b+a')}$. In addition, chiasmas may occur (1) between dividing homologues, or (2) between dividing non-homologues. (Cf. Belling, 1933.)

p. 310, b. "Repulsion .... able to break one of the four." This is conjectural. Observational proof is needed that four attachments are first formed.

p. 311, t. "Chiasmas are first seen through the opening of loops separating pairs of chromatids at diplotene." Chiasmas are first seen at late pachytene, before any opening of loops (McClintock, 1931; Belling, 1931, and MS).

p. 311, t. "Their position cannot be accurately recorded at the very moment of origin." It can be told at zygotene, with some probability.

p. 311, t. "The change cannot be observed in living nuclei." Why not? They can be kept alive for days. Belar has observed diaphase (1929*a*), and I have studied leptotene and pachytene in living nuclei.

p. 311, b. "Observations of meiosis are usually confined to metaphase." Most lithographic and other plates have seemed to show, or tried to show, the whole sequence from leptotene to telophase.

p. 313, t. "Terminal origin of chiasmas." On my theory of crossing-over, a terminal chiasma cannot arise or exist.

p. 314, b. "Frequency proportionate to the length." This "proportion" I do not consider true proportion.

p. 317, t. "The terminal connection between pairs of chromosomes can always be seen to be double in favorable material." It is often single in the best smears. But the same may be said of the fiber joining a satellite to the chromosome body, during meiosis or mitosis; and this does not show "change of partner." These terminal fibers are apparently new formations, not part of a chiasma.

p. 318, t. "Where the association .... fails." Observational proofs that the junction previously existed are needed here.

p. 319, t. "Implies that the terminal association is a chiasma." The microscope shows that it is not, I think.

p. 327, b. "Prophase" here = early, middle, and late diaphase.

p. 329, m. "Compensating" = "similar." "Non-compensating" = "unlike."

p. 329, b. "Theory that meiosis is a precocious mitosis." Theory = conjecture, and is apparently incapable of proof.

p. 333, m. "Terminal affinity can only .... develop after the beginning of diplotene." On this hypothesis, bivalents in any species which did not open out at the diplotene stage would remain united by their ends when they subsequently opened out. There need then be no chiasmas for such union to arise.

p. 333, m and b. This "terminal affinity" may be the fiber-forming capacity of the terminal chromomeres, which is possessed in some degree by all chromomeres.

p. 338, t. "The .... repulsion .... found .... at the beginning of anaphase in mitosis." There seems not to be sufficient proof of repulsion rather than traction here. See Belar on *Tradescantia* mitosis (1929). There is often a fine fiber projecting near the attachment chromomere, which points to "traction."

p. 338, m. "If the repulsion is electrical." Experimental proof is wanted. References to experiments are needed, if it is more than a conjecture.

p. 340, m. "Repulsion being .... magnetic." This is probably a conjecture, I think.

p. 341, t. Repulsion between spindle attachments and the poles is not evident to me. References to observations seem needed, if this is more than a conjecture.

p. 342, m. "Attractions .... chemically specific." Why not physically too, if the gene is made of more than one molecule?

p. 342, b. Repulsion at prophase in mitosis is not clear to me. References to experiments or observations are needed, unless this is a conjecture.

p. 343, b. "Crossing-over .... before we bother ourselves as to how it occurs." But others are working to show this, and so the statement does not seem altruistic.

CHAPTER 13

p. 344, m. "Dissimilarity of structure." This may refer to (1) presence of secondary constrictions or satellites, or (2) differences in gene arrangement (heterosomy), or (3) differences in alleles (heterozygosis).

p. 348, b. "The distal parts .... are precocious." Why not, "the proximal parts are late"?

p. 350, b. "Without very clear evidence of constancy." Such very clear evidence of constancy is not apparently demanded from the authors quoted on pages 348 and 349. Heitz's evidence seems to be against the precocity conjecture.

p. 352, t. "It is probable that the property of asynapsis is here due to failure of chiasma formation." But on page 334, this same phenomenon in asynaptic maize was ascribed to the combination of "complete terminalization" and "no terminal affinity."

p. 355, t. "Structural differences" = heterosomy. It is not yet known whether heterozygosis of alleles affects synapsis or chiasma formation. Heterozygosis of the terminal chromomeres might or might not prevent terminal junctions.

p. 361, t. "This perfected mechanism had arisen in hybrids." A conjecture, apparently.

p. 364, b. "In *Datura* the proportions .... are very variable." This may be because many cells were examined by me.

p. 371, b. "The origin of the system does not present much difficulty." Not for a conjecture.

p. 372, t. "Polarization." In quite young triploid Daturas I found that the first buds sometimes gave numbers of *24* + *12* chromosomes at second metaphase, above the chance ratio.

CHAPTER 14

p. 379, t. "Equally homozygous." They may be heterozygous for many alleles. Homosomic is better.

p. 379, t. "Structurally distinguishable" = visibly different. They are heterosomic in *Drosophila.*

p. 379, b. "The X and Y chromosomes differ," i.e., in appearance.

p. 392, m. "Small fourth chromosome .... has arisen by fragmentation of the X." This unproved conjecture does not account for its having a fusal chromomere.

p. 395, t. "Sex chromosomes that appear to have paired normally during prophase." Synapsis has not been thoroughly studied here, I think.

p. 395, b. A third possibility may be that chiasmas and crossing-over are absent or rare, and terminal junctions prevail.

p. 396, t. "When crossing-over in *Drosophila* is genetically reduced." Presumably by inversions, and the locality of the reduction depends partly on the locality of the inversion.

p. 396, t. "Reciprocal crossing-over .... is unduly frequent in the X chromosome." (Reciprocal crossing-over is from a pair of similar chiasmas and = supplemental crossing-over.) In my opinion this conjecture is dubious, for it seems to require crossing-over between sister chromatids—which has not been proved (cf. L. V. Morgan, 1932; and *in litt.*).

p. 396, t. "The chromosomes seem to pair normally at zygotene and have non-terminal chiasmas at metaphase." I cannot deduce these results from the paper of Guyénot and Naville (1929), or from Huettner (1930).

p. 398, b, 5. "The extreme stages.... may be contrasted in the following way." Table 58 is presumed to follow here.

p. 398, b. "Complex heterozygote" = balanced heterosomic.

p. 407, b. "Translocation of small pieces from one chromosome to the middle of another." This is "insertion," and is apparently rare.

p. 408, t–m. "Translocation of a segment *x* from a chromosome *AxB* to another chromosome *CD*," to make *CxD*. "Insertion" is meant.

p. 409, t. Reciprocal translocation (segmental interchange) may also be due, on my theory, to crossing-over between non-homologues, like translocation and insertion.

p. 409, b. "Interchange occurs.... through the entanglement of two chromosomes at pachytene." This is a plausible conjecture, but unproved. It could not well account for translocation, inversion, insertion, deletion, or deficiency.

p. 411, b. "This orientation can be supposed to be due to the force of repulsion between attachment constrictions." In my judgment, this should straighten out the ring, not form it into alternative *V's*. The repulsion should repel laterally also.

CHAPTER 16

p. 449, b. "The chromosomes.... consist essentially of constant materials." If this means the metaphase chromosomes, I do not agree. The gene string (or the chromonema) alone is a fairly persistent structure.

p. 450, m. "Linear order which is liable to change.... from undefined causes." It changes by translocation, inversion, interchange, deletion, insertion, etc.

p. 451, t. "Property of occasionally reproducing dissimilar particles." Not proved.

p. 451, t. Point mutation seems due (according to experiments *ad hoc*) to photons or electrons, not to undefined causes.

p. 451, m and b. This is mainly conjecture, I think.

p. 452–453. This seems mostly conjectural to me. A few *unexpected* new facts might upset much of it, I think.

p. 455–477. There seems to me much conjecture here. I consider such speculations barren, and harmful to cytology, and suspect that half of them may prove erroneous. "Which half" we do not know.

p. 478, t. "Best observed cytologically." This is doubtful to me. Inversion, translocation, etc., were mostly first discovered genetically.

p. 478, t. "Proportion change is often advantageous." This seems so because the author uses a conjecture as to insertions and translocations (duplications) that does not seem proved. "Often" is dubious. "Proportion" should not include rearrangement.

p. 479, m. "Gene mutation . . . . is a property inherent in gene propagation." It has been proved that gene mutation is normally caused by short-wave radiation of certain frequency. There is no proof that it is related to the division of genes.

p. 486, m–b. Comparison of living and fixed material "is necessarily of restricted use with the ordinary microscopic technique." One cannot, in my judgment, properly study artifacts without preliminary study of living chromonemas and chromosomes. The author's apparent lack of first-hand knowledge of the karyology of living chromosomes seems to injure his interpretation of artifacts.

p. 486, b. "Photographs of living cells" taken with ultraviolet light. Perhaps these cells were not always examined after the photographs were taken to see if they had been killed by the intense illumination.

p. 488, m–b. The author's "non-characteristic artifact" = (in the usual terminology) "artifact." The author's "characteristic artifact" = "absence of artifact."

p. 488, b. "Differently hydrated particles" in the spindle. References to experiments are needed here, unless this is speculation.

p. 489, t. "It is assumed that the chromosome complement seen at one division is characteristic." Most cytologists, in my experience, examine many divisions. The exceptions (as tetraploid tissue in root tips, or double pollen grains) are important.

p. 490, t. "Comparative inference . . . . Hypothesis based on it has often proved more reliable than the 'facts' of direct observation." This turns on the meaning of "reliable." Wrong conjectures are perhaps in the majority, but have often to wait years before being proved false. Erroneous observations (though the bane of a science) are few, and are often quickly found out.

p. 491, b. "The plant cytologist has been able to contribute the great bulk of recent advances." There may be two opinions about this. If one holds that karyology is a dead body of which the life is genetics, one would rank high the combined genetic and cytological work done with animals, including segregation, crossing-over, non-disjunction, attached X's, translocation, inversion, reciprocal translocation, insertion, duplication, triploidy, interference, mutation, gene balance, and sex.

REPLY BY C. D. DARLINGTON

I thank Dr. Belling for publishing the results of a detailed examination of my book. His remarks are of various kinds. Some are differences of opinion, which are sufficiently discussed in the book. Others are corrections, which I partly or wholly accept and will incorporate in any later edition. The student may therefore find the following classification useful.

A. *Acceptable criticisms*

1. Notes of misprints (235, 398, b^5)*
2. Corrections of errors or omissions of reference (20, t; 34, t; 35, t; 43, t; 80, t; 118, b; 165–6; 231 (table); 372, t)
3. Additions of unpublished or newly published evidence (17, b; 20, t; 93, b; 100, t; 245, t; 286, t; 288, b; 290, t; 311, t)

B. *Remarks requiring no further discussion*

4. General comment and expansions of condensed statements (e.g., 294, t; 301, m)
5. Misunderstandings of condensed statements (e.g., 116, t; 131, b; 132, t; 491, b)
6. Criticisms of method of expression (e.g., 95, b; 237, m; 279, m)

C. *Remarks requiring further discussion*

7. Criticisms of interpretation of published or direct observations (e.g., 90; 114, b). Cf. Appendix I

With regard to interpretation, Belling's criticisms rest upon the greater weight he attaches to direct observation and the lesser weight he attaches to comparison of related observations. For example, his opinion that the apparent association of three threads is of importance at pachytene in the triploid (114, b *et al.*), in opposition to my view that effective association is only between pairs. The evidence for my view has been given in anticipation of this objection. It consists in the frequency curve of chiasmata in individual chromosomes in triploids (D. & Mathes, 1932).

8. Criticisms of terminology (91, m; 129; 278, m)

With regard to terminology, I have tried to use simple terms such as "pairing" (91, m) to describe events for which a number of technical terms have been used in the past, for the reasons given in

---

* Also, p. 466, *for* Vitamin D *read* Vitamin C.

Appendix III. I have, by mistake, used the word "hybrid" twice in the taxonomic sense which cannot, in my opinion, be consistently applied in the light of our present knowledge of genetics (129 and 278, m); "non-hybrid triploids" should read "triploids of non-hybrid origin," since all triploids are numerical hybrids. Similarly, cytological hybrids do not all show hybrid vigor.

9. Criticisms of conjectures. Cf. Appendix VI.

Belling has criticized my conjectures. We both make conjectures and describe them formally as hypotheses. The difference again arises from the opposition between the morphological and analytical points of view dealt with in Appendix VI. Belling maintains the morphological point of view, of which he is the ablest exponent. I maintain the analytical point of view, namely: every student should be aware of the conjectures that may reasonably be made in regard to the causes of the events he is studying. I maintain it partly, perhaps, because to me the cause is more real than the event itself. If the student is unaware of these conjectures he is apt to consider his present state of knowledge as unchangeable as the laws of the Medes and Persians. And he cannot be blamed for this error; it has been shared for over twenty years by some of our leading cytologists. But there is now no longer any excuse for it.

C. D. D.

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THE LIFE-HISTORY OF PTERYGOPHORA CALIFORNICA RUPRECHT

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THE LIFE-HISTORY OF PTERYGOPHORA CALIFORNICA RUPRECHT

BY

HAZEL HAYDEN McKAY

INTRODUCTION

This paper presents an account of the life-history of *Pterygophora californica* Ruprecht based upon both morphological and cytological data, giving special attention to the development and behavior of the male gametes and to the process of fertilization.

In recent years many studies on the life-histories of various members of the Laminariales have been made, including, in some of the later papers, the cytological evidence for the alternation of generations. The reproductive organs of the Laminariales were first studied by Thuret (1850) who considered the product of the unilocular sporangia to be zoospores. Williams (1900) also considered these motile spores to be asexual and in his very brief article described the production of a "branched protonema-like structure" from the germinating zoospores. Thus the Laminariales were looked upon as a group of plants reproducing only by means of asexual zoospores until Drew (1910), after working with *Laminaria digitata* Lamour. and *Laminaria saccharina* (L.) Lamour., declared that the so-called zoospores were isogametes which fuse, and that the cells resulting from their fusion germinate and produce filamentous structures from which the adult plants develop. Killian (1911) agreed with Drew in these conclusions, but Williams (1912) rejected Drew's view on account of evidence obtained from his study of *Laminaria saccharina.* Williams (1912) confirmed his previous work (1900) and again described the swarm spores as asexual zoospores which germinate without any fusion, producing protonematoid structures which eventually give rise to the young *Laminaria* plants. These studies of Drew, Killian, and Williams suggested further investigation of the subject and led to Sauvageau's (1915, 1916*a*, 1916*b*) illuminating studies of *Sacchoriza bulbosa* De la Pylaie, in which a definite alternation of generations was demonstrated. Sauvageau found the macroscopic plant to be the sporophyte generation, bearing zoospores which upon germination give rise to the microscopic gametophytes bearing oogonia and antheridia, and that, subsequently, the fertilized egg produces the macroscopic generation. He observed oogonia and antheridia on the dioecious gametophytes but did not distinguish the male gametes or observe the process of fusion. Closely following this work, Sauvageau (1916*c*) published a study of *Alaria esculenta* Grev. in which he found a similar alternation of generations. In the same year Kylin (1916), working independently in Sweden, published the results of his researches on *Laminaria digitata* Lamour., confirming the results of Sauvageau in all essential particulars. Again Sauvageau's (1916*d*, 1918) studies on *Laminaria flexicaulis* le Jolis, *L. Lejolisii* Sauv., *L. Cloustonii* Edmon., and *L. saccharina* gave evidence of an alternation of generations in the Laminariales. Kuckuck (1917) and Pascher (1918) also made similar studies on *L. saccharina* and added to our knowledge of the reproduction in this group by describing the production of zoospores from the young sporophyte. Yendo (1919) published a monograph on the genus *Alaria* in which he included a description of the gametophytic generation of *Alaria crassifolia* Kjellm., which also confirmed the results of previous studies on the life-histories of the Laminariales. Still later, Ikari (1921) described the similar development of *Laminaria religiosa* Miyabe.

Since then the following investigations have added to our knowledge of the process of alternation of generations in the order: Brandt (1923) reported on the life-history of *Macrocystis pyrifera* (L.) Ag.; Williams (1921) made a preliminary study on *Laminaria* and *Chorda;* Myers (1926 and 1928) described the alternation of generations in *Postelsia palmaeformis* Rupr., *Laminaria Sinclairii* (Harv.) Farl., and *Egregia Menziesii* (Turn.) Aresh.; Ikari (1927), *Ecklonia bicyclis* Kjellm.; Angst (1927 and 1929), *Costaria costata* (Turn.) Saund., and *Pleurophycus Gardneri* Setch. and Saund.; Hartge (1928), *Nereocystis Luetkeana* (Mert.) Post. and Rupr.; and Ueda (1929), *Laminaria religiosa.* Delf and Levyn (1926) in a preliminary study on *Macrocystis pyrifera* made the important discovery that zoospores of two sizes are produced in the zoosporangia of this species—in contrast to the homosporous condition found in all other members of the Laminariales previously studied. These heterozoospores of *Macrocystis* germinate and give rise to gametophytes of two sizes, the larger of the zoospores producing the larger female gametophyte, while the smaller zoospore produces the smaller male gametophyte.

The first attempt to study the chromosome number in the different phases of the life-history of the Laminariales was made by Kylin (1918) in his work on *Chorda filum* (L.) Stachk. In addition to studying these stages in the course of development of this species which had previously been described for other members of the group, Kylin established the fact that reduction in the chromosome number takes place in the first division of the zoosporangium nucleus, and that the haploid number of chromosomes for this species is 20. Another contribution to this phase of the subject is the work of Myers (1928) on *Egregia Menziesii.* She traced the development of the dioecious gametophytes from the zoospores, and described somatic mitosis in the sporophyte, reduction of the chromosome number in the zoosporangium, and the division of the nucleus in the young gametophytes. In general her results confirmed those of Kylin, in that the macroscopic plant was found to be diploid and in that reduction division takes place in the first division of the zoosporangium nucleus. She found that the chromosome number of the sporophyte is 16, and that 16 chromosomes are evident at the metaphase of the first nuclear division on the sporangium initial, while 8 are present at the metaphase of the second division. The chromosome number of the gametophyte generation was demonstrated in the first nuclear division of the germinating zoospore, where 8 chromosomes are evident at metaphase.

Although frequent references have been made to the male gametes of the Laminariales, no complete description of their structure has yet been given. In a preliminary paper unaccompanied by illustrations Williams (1921) described briefly the liberation of the male gamete from the antheridium and several stages in the fusion of the male and female nuclei in the egg of *Laminaria.* In his work on *Laminaria religiosa,* Ueda (1929) also reported seeing the male gametes escape from the antheridium. He described them as measuring 4.5 by 3.5μ, and light yellowish in color but with no chromatophore and no stigma. The process of fertilization was not observed, however, the male gametes were not figured, and nothing was said in regard to their locomotion. Myers (1928) did not find the male gametes of *Egregia Menziesii,* although in cultures producing young sporophytes the empty antheridia were abundant. Likewise, in cultures where no empty antheridia were found, no sporophytes developed in spite of the fact that many eggs were discharged. Both this and the cytological evidence indicate the necessity for fertilization, although neither the male gametes nor the actual fusion were observed, nor was the chromosome number determined in the young sporophytes produced in culture.

PTERYGOPHORA CALIFORNICA *RUPRECHT*

GENERAL DESCRIPTION

The name of the genus *Pterygophora* was first used by Ruprecht (1848) when he described the structure of the stipe in connection with similar studies on other members of the Laminariales. He stated that *Pterygophora* was an intermediate form between *Capea (Ecklonia)* and *Alaria* but he did not give a description of the genus at this time. Later Ruprecht (1852) described *Pterygophora californica* from specimens collected near Fort Ross, California, by Wosnessenski in 1840. Since that time, no other species of this genus have been described and *Pterygophora* now stands as a monotypic genus in the order Laminariales, family Alariaceae, and tribe Alarieae (Setchell and Gardner 1925).

The sporophyte generation of *Pterygophora californica* is one of the larger, more sturdy members of the Melanophyceae found growing along the Pacific Coast of North America and, at the present time, is known to occur from Vancouver Island to Lower California. It grows attached to rocks in the wave-swept portion of the sublittoral zone where it is completely submerged except at extremely low tide. The plant body consists of stout much branched hapteres, a solid woody stipe, lateral sporophylls, and a terminal blade. The stipe is terete at the base, becoming gradually flattened toward the upper end until it appears distinctly flat at the transition region between the stipe and the blade. The single long, expanded blade borne at the tip of the stipe shows an indication of a midrib in the thickened central region. The sporophylls, 18 to 20 in number, are produced laterally from the transition region of the stipe. The plants in the San Francisco Bay region range from 1 to 3 meters in length and bear sporophylls from .5 to 1.5 meters long.

The sporophyte generation of Pterygophora is perennial. Approximately twenty sporophylls are produced annually, fruit, and finally disintegrate, leaving a series of small scars along the margins of the stipe at the flattened transition region. The new sporophylls develop above, being produced during the growing season of each year as lateral projections from the transition region of the stipe. By observing the number of these sporophyll scars Frye (1918) has estimated the age of the plants found growing in the Puget Sound region. He determined this by dividing the total number of scars on the stipe plus the number of sporophylls present on the plant, by the number of sporophylls produced during a single year. This result corresponds with the number of rings found in a cross-section of the stipe at a region 25 mm. from the base. After making many such determinations he concluded that these rings were formed annually and that the plants may live as long as thirteen years. MacMillan (1902), who also studied *Pterygophora californica* in the region of Puget Sound, has estimated that some of the plants may live as long as 25 years.

The sori are borne as irregular patches on both sides of the sporophylls and may cover the greater portion of the surface or only a small part of it. The plants in the localities from which my studies were made bear fruiting sporophylls to some extent throughout the entire year. Growth starts in the transition region during February and new sporophylls are produced from that time on throughout the entire summer. The old sporophylls from the previous season remain as ragged remnants covered with epiphytes until midsummer when they are mostly worn away.

The sporophylls produced in February begin to fruit during the following September and October and continue to produce sporangia until they are worn or torn away. It is possible to obtain sori in abundance at all times of the year with the exception of a period from the first of July to the last of September, when they are very scanty or found so nearly covered with epiphytes that cultures made from them are not successful.

MATERIALS AND METHODS

The material used in this investigation was collected near Duxbury Reef, Marin County, and at Moss Beach, San Mateo County, California. Collections were made throughout a period of two years at intervals approximately a month apart. The sporophylls and the somatic material to be used for the cytological investigation were cut into small strips and placed in the fixing solutions at the beach. The fixing solutions employed were Navashin's solution made up in sea water, Bouin's solution, and a modified Flemming's solution made up as follows:

Flemming's solution—

Chromic acid	1 gram
Glacial acetic acid	2 cc.
Osmic acid (1%)	3 cc.
Sea water	100 cc.

Osmic acid is added as solution is used.

The Navashin's solution—

Solution A

Sea water	65 cc.
Glacial acetic acid	10 cc.
Chromic acid	1 gram

Solution B

Sea water	35 cc.
Commercial formalin	40 cc.

Equal quantities of solutions A and B are mixed immediately before placing the material in the killing fluid.

The best results were obtained from the material fixed in the modified Flemming's solution, although that fixed in the Navashin's solution gave good results in most cases; that fixed in the Bouin's solution stained sharply but the cell contents were badly distorted.

The material was left in the Flemming's solution for a period of from 24 to 48 hours and washed first in sea water, then in equal parts of sea water and fresh water, and finally in fresh water, during a period of 12 hours. The regular schedule of dehydrating and embedding in paraffin was followed with the exception that benzol was substituted for xylol in the process. Benzol was found to be valuable since it caused less distortion of the cell contents than xylol.

Microtome sections 3 to 5μ in thickness were cut and mounted on slides by means of albumin fixative. Before staining, the material was bleached by submerging the slides in a dilute solution of hydrogen peroxide which was then placed in the bright sunlight for thirty minutes. This process interfered with further manipulation since it tended to loosen the sections from the slides. Nevertheless, it was a necessary step, especially in staining the sporophylls, since the contents of the zoosporangia were blackened by the fixing solution to an extent that made it impossibe to study the nuclear behavior without bleaching.

Although several staining methods were tried, Haidenhain's iron-alum haematoxylin was found to give the best results in all cases. The following staining schedule proved to be the most satisfactory for the zoosporangia and somatic cells:

Staining schedule—

Iron-alum, 2 per cent solution	2 hours
Distilled water	Several changes during period of 30 minutes
Haidenhain's haematoxylin, ½ per cent solution	18–36 hours
Running tap water	30 minutes

Destain in—

Iron-alum, ½ per cent solution	Until sufficiently differentiated (about 30–40 minutes)
Running tap water	30 minutes
Alcohol, 100 per cent	1 minute
Clove oil	5–10 minutes

Then mount in balsam

It was found that overstaining the material and then destaining slowly yielded the sharpest and most distinct figures.

For the study of the germinating spores and the gametophytes a similar method gave satisfactory results. The chrom-acetic-osmic fixing solution recommended for marine algae by Chamberlain (1928) was employed. The slides bearing the attached sporlings were left in the fixing solution for one hour, and stained according to the previously described schedule except that a saturated solution of picric acid was used for destaining in place of the ½ per cent iron-alum solution. The picric acid proved to be of value in this process since it removed the excess stain from the chromatophores and cytoplasm more rapidly than from the chromatin of the nucleus, thus leaving the nuclear structures in good condition for study.

The culture methods used are similar to those employed by Myers (1926) and Angst (1927), and described by Kufferath (1929) for culture work with marine algae. Pieces of the fruiting sporophylls were washed thoroughly in sterilized sea water using a stiff brush in order to remove, as nearly as possible, all foreign matter which adheres to the gelatinous surfaces. The sides of glass culture dishes were lined with slides standing on end, culture solution was added, and a fragment of the sorus about one centimeter square was placed in each dish. These were allowed to stand over a period of from 12 to 24 hours before the sporophyll tissue was removed. These culture dishes were placed in a glass-enclosed chamber situated on the north side of the building where it was never exposed to direct sunlight. The temperature ranged from 10° to 15° C. Under these conditions the zoospores escaped from the zoosporangia, swam about for a time, and settled down on the slides where they became attached and germinated. These slides could be removed at will and examined under the microscope, or could be prepared for future study by fixing and staining.

The culture solution used was made up of filtered sea water, sterilized in the autoclave at 15 pounds pressure for 30 minutes, to which was added traces of sodium nitrate, calcium chloride, and potassium hydrogen phosphate. Before placing in the culture dishes, the solution was aerated by shaking vigorously in a flask. The nutrient solution was renewed once a week during the growth period of the gametophytes.

SOMATIC MITOSIS

The material used for the study of somatic mitosis was collected during February to June, a period when the process of rejuvenescence is taking place. Small portions of the meristematic region at the upper end of the stipe and material from the young rapidly growing sporophylls were fixed in the modified Flemming's solution, dehydrated, embedded in paraffin, sectioned at 3–5μ, and stained with Haidenhain's iron-alum haematoxylin according to the method already described.

The meristematic or transition region of the stipe is composed of a number of well defined layers, as seen in a transverse section. The medulla is made up of anastomosing filaments intermingled with two long trumpet-shaped cells both of which contain deep staining granular material. This region is surrounded by a thick cortex composed, in the inner part, of regular hexagonal cells and toward the periphery, of smaller rectangular cells in which chromatophores are abundant. The third, the peripheral region, is made up of several rows of smaller rectangular deeply colored cells. The inner cortex was found to be the most satisfactory for the study of mitotic figures since in this region the cytoplasm stained lightly and fewer chromatophores and cell inclusions were present to obstruct the view.

In the resting cells of the inner cortex the nuclei are very small, measuring approximately 3μ in diameter, the nucleolus is small but deeply staining, and the reticulum so exceedingly delicate that it is scarcely distinguishable. The large vacuoles and the dense cytoplasm surrounding the nucleus are conspicuous features of these cells (pl. 9, fig. 1).

In the early prophase of division the nucleus increases in size until it is from two to three times the original diameter. The nucleolus enlarges in proportion and a definite reticulum bearing small clumps of deeply staining chromatin granules becomes apparent (pl. 9, fig. 2). As mitosis progresses, conspicuous chromatin knots appear at the junction of the fibrils of the reticulum where they increase in size and decrease in number, eventually forming the chromosomes (pl. 9, figs. 3 and 4). The connecting fibrils become more and more indistinct until, at late prophase, they remain as short fragments attached to the chromosomes or are no longer evident, thus leaving the chromosomes free in the nucleoplasm (pl. 9, figs. 6 and 7). The nuclear membrane is visible throughout prophase and may disappear either at metaphase or early anaphase. The nucleolus gradually becomes lighter colored as mitosis progresses and disappears in late prophase as the chromosomes are formed.

A polar view of metaphase in which the twenty-six chromosomes, arranged in the equatorial plate, are actually splitting is shown in plate 9, figure 5. The nuclear membrane is no longer evident. A lateral view of early anaphase (pl. 9, fig. 10) shows the achromatic figure, consisting of definite spindle fibers, a small spherical deep-staining centrosome at each pole, and an indication of a few astral rays. By the various methods of fixing and staining used in this study, the centrosomes were made evident only at metaphase and early anaphase. Here they stain sharply and are surrounded by centrospheres of densely granular material and a relatively few inconspicuous astral rays. This situation is comparable to that observed in *Cutleria* by Yamanouchi (1912) where the centrosomes could be detected only at metaphase and early anaphase. In his work on the tetraspore mother cells of *Dictyota dichotoma,* however, Mottier (1900) found conspicuous centrosomes and traced their behavior throughout mitosis, demonstrating that they are handed on from nucleus to nucleus in division. In his study on *Stypocaulon* and *Sphacelaria* Swingle (1897) also was able to demonstrate the presence of the centrosomes and distinct asters in all stages of the division process, showing that they divide before the chromosomes and establish the poles of the spindle.

The chromosomes all measure less than 1μ in length and vary but slightly in size and shape. In a study of the metaphase plate it is possible to distinguish three pairs of short rod-shaped chromosomes, nine pairs ovoid in shape and of various sizes, and one pair of minute spherical chromosomes. The largest rod-shaped pair measures about .8μ in length, the ovals from .3 to .6μ in the longest diameter, and the small spherical pair are very near the limit of vision (pl. 11, fig. 7).

In anaphase the two halves of the split chromosomes migrate toward opposite poles being held close together in clumps but distinct from one another until they reach the region of the poles (pl. 9, figs. 8 and 9). During telophase they coalesce and lose their identity by gradually becoming granular and taking the stain less readily (pl. 9, fig. 11). The spindle remains throughout anaphase and disappears as the chromosomes become aggegated at the poles. The spindle fades away first in the equatorial region but remains in the vicinity of the chromosome groups until the nuclear membrane is formed around the daughter nuclei.

The cell plate between the daughter nuclei may be formed shortly after the chromosomes have migrated to the poles or, as is more often the case, cytokinesis does not occur until the nuclei divide a number of times. The two daughter nuclei resulting from division are often not transformed into the resting state, but pass quickly from early telophase to a prophase condition and divide again. As a result, cells are often found with from four to eight nuclei and in these cases all of the transverse walls are laid down simultaneously (pl. 9, figs. 12 and 13). The cell plate seems to be formed as a result of the accumulation of dense granular cytoplasm in the central region between two nuclei and is entirely independent of the spindle fibers (pl. 9, figs. 7, 8, and 13). A similar method of septation has been described in a number of instances among the brown algae. Mottier (1900) in his work on *Dictyota dichotoma* describes a localization of material in the cytoplasm, which resulted in cell plate formation. Strasburger (1897) reported that in

Fucus serratus the cell plate is formed by an accumulation of small granules, as did Yamanouchi (1909) in his study of somatic mitosis in *Fucus.*

DEVELOPMENT OF THE ZOOSPORANGIA

In *Pterygophora* the zoosporangia are borne in irregular shaped, dark colored sori which occur on both surfaces of the sporophylls. The sorus is made up of a palisade-like layer of sterile paraphyses and fertile sporangia borne side by side. Both of these organs originate from the superficial cells of the sporophylls by two successive divisions (pl. 11, fig. 11). The typical diploid number of chromosomes is evident at the metaphase of the first division of the superficial cell by which the paraphysis is formed (pl. 11, fig. 12). Again, a similar number is found when the superficial cell divides the second time giving rise to the sporangium initial cell (pl. 11, fig. 13).

The resting nucleus in a very young sporangium initial cell closely resembles the nucleus of the somatic cell, being about 3μ in diameter, and containing a distinct nucleolus and a very delicate reticulum (pl. 10, fig. 1). The zoosporangium reaches approximately one-half the mature size before the first nuclear division occurs. The first indications of the approaching division are the enlargement of the nucleus and the formation of a conspicuous network of anastomosing granular fibers bearing deeply staining clumps of chromatin at the junction of the threads (pl. 10, figs. 2 and 3). This is not unlike the condition found in the somatic mitosis (pl. 9, figs. 2 and 3). Some of the threads thicken, becoming more compact and homogeneous in nature as others break and disappear, thus forming a network of larger meshes. The network is converted into a spireme as more of the connecting threads lose their color and disappear while others become thicker and deeper in color (pl. 10, fig. 4). This process continues until the chromatic material is arranged in a thick spireme. The spireme is not continuous but is composed of several long thick threads which appear to be single in nature since, in no place, could two threads lying side by side be traced to any distance. The spireme contracts and becomes aggregated in synizesis as a dense mass of loops at one side of the nuclear cavity where it lies in contact with the nuclear membrane (pl. 10, figs. 5 and 6). The spireme is evident only in the first division of the nucleus in the zoosporangium initial cell and is never found to occur in the mitotic divisions of either sporophyte or gametophyte. A comparable situation has been found in *Pylaiella littoralis* (Knight 1923) and *Cutleria multifida* (Yamanouchi 1912) in which there is no indication of a spireme except during reduction division. In *Dictyota dichotoma,* however, Mottier (1900) found a behavior quite contrary to this in that no spireme was found in the prophase of reduction division but that the chromosomes arise as isolated masses or clumps. Also, in the vegetative cells of *Dictyota* there is developed a typical spireme similar to that found in the somatic mitosis of higher plants.

In *Pterygophora* the characteristic looping of synizesis is later followed by a contraction of the threads, resulting in a definite number of chromosome units which lie free in the nucleoplasm (pl. 10, figs. 7 and 8). These chromatin masses move apart forming irregular *X*-, *O*-, and *V*-shaped figures, the diakinesis configuration involving the 13 bivalent chromosomes (pl. 10, figs. 9 and 10, and pl. 11, fig. 8). During the late prophase stages the nucleolus becomes lighter in color and irregular in shape, appearing as an inconspicuous remnant at diakinesis. The fact that very few diakinetic figures were seen in these studies indicates that this stage is of short duration as compared with the other phases of nuclear division.

At metaphase the bivalent chromosomes are arranged in an equatorial plate, a side view of which shows the achromatic figure. There is a distinct spindle and, at each pole, a deeply staining centrosome surrounded by a cap of dense cytoplasm (pl. 10, fig. 13). The chromosome pairs, as they are seen in a polar view of this plate, appear to be constricted at the middle as though the bivalent partners were joined together end to end (pl. 10, figs. 11 and 12). This constricted condition as shown again in plate 10, figure 10, may be interpreted as representing an early anaphase condition preceding disjunction of the thirteen bivalent chromosomes in which each small dumb-bell-shaped figure represents a pair of univalent chromosomes. They disjoin at the constriction, one partner passing to each pole, and thus bring about the reduction in the chromosome number, so that, in all subsequent divisions in the zoosporangium, thirteen univalent chromosomes are present. The principal features which distinguish the reduction division from the somatic mitosis are the distinct spireme, the synizetic knot, the diakinetic configuration, and the thirteen large bivalent chromosomes evident at metaphase.

The reduction division is quickly followed by the second division, which is identical with somatic mitosis (pl. 10, figs. 14, 15, and 16). The two nuclei usually divide simultaneously but occasionally in succession. Thirteen univalent chromosomes, the reduced number, are present at late prophase and metaphase (pl. 10, fig. 14, and pl. 11, fig. 9). The third division follows the second closely and the thirteen chromosomes are again evident at metaphase (pl. 10, fig. 18). Nuclear division continues in a similar manner until there are approximately 32 nuclei in the sporangium. The direction of the axis of the spindle is either in the direction of the long axis of the sporangium or slightly oblique, but seldom perpendicular to it.

The chromatophores, which range in number from two to six in the sporangium initial cell, begin to divide at about the time the four-nucleate stage is reached. One chromatophore soon becomes associated with each nucleus, which may be evident as early as the eight-nucleate stage (pl. 10, fig. 19). The chromatophores continue to divide simultaneously with the nuclei, so that, by the time the 32-nucleate stage is reached, a corresponding number of chromatophores are present, one closely applied to each nucleus (pl. 10, figs. 19–26).

Soon after the 32 nuclei are formed, cleavage furrows appear in the cytoplasm between the nuclei. Cleavage is accomplished by the joining together of small vacuoles in a definite region between the nuclei, resulting in the division of the cytoplasmic mass into a definite number of uninucleate units. This method of cleavage is not unlike that described by Harper (1899) for certain members of the Mucorales where the division between the columella and the rest of the sporangium is formed by the coalescence of a dome-shaped layer of small vacuoles. In one instance among the flowering plants, a similar situation has been observed by Castetter (1925) in his study of cytokinesis in the microsporocyte of *Melilotus alba.* In this case the quadripartition of the pollen mother cell is effected by means of furrows which are formed by the fusion of a series of vacuoles and without any indication of the formation of cell plates across the equators of the spindles.

As the cleavage furrows appear in the zoosporangium of *Pterygophora californica,* the cytoplasm draws away from the wall, thus leaving the 32 zoospore primordia crowded tightly together toward the central region of the zoosporangium (pl. 10, fig. 26). In addition to a small amount of cytoplasm, each primordium contains one chromatophore and one nucleus. The entire cytoplasmal content of the zoosporangium is used up in this process of zoospore formation. As a result 32 zoospores are usually formed in each sporangium, although quite commonly the nuclei and chromatophores divide again and give rise to 64 zoospores. Never more than 64 zoospores have been found to occur in a single sporangium in the material collected in the San Francisco Bay region. This does not confirm the observations made by MacMillan (1902) on the material collected in Puget Sound. He states, "The sori are composed of numerous saccate gonidangia, each bearing from 50 to 200 spherical gonidia."

As the zoospores develop, the wall at the apex of the sporangium gradually becomes thickened, forming a conspicuous cap. At about the time the cleavage furrows are produced, this cap begins to swell and separate into layers, eventually breaking down by means of the formation of one or more longitudinal clefts (pl. 10, fig. 26). A beak-like opening results through which the zoospores pass out, one by one, into the surrounding medium where they disentangle their cilia and swim rapidly away.

GAMETOPHYTES

The zoospore is distinctly pyriform in shape and contains a conspicuous lobed chromatophore with which is associated a large red eyespot. There are two lateral cilia of different lengths, the longer one pointing in an anterior direction and measuring approximately 18μ in length, while the shorter one points in a lateral or posterior direction and measures about 6μ in length. The zoospores are homosporous and range in size from 6 by 9μ to 7 by 11.2μ when in the motile condition (pl. 12, figs. 1 and 2). After the zoospores swim about for a time they withdraw their cilia, become spherical in shape, and measure from 6 to 8μ in diameter (pl. 12, figs. 3 and 4). These are much larger than those recorded for *Pterygophora* by MacMillan (1902), who found the spherical gonidia to be 2μ in diameter.

When placed in the artificial culture solution the zoospores swim actively for from 30 minutes to 4 hours and then attach themselves to some surface, withdraw their cilia, round up, and secrete a distinct wall (pl. 12, figs. 3, 4, and 5). Germination begins almost at once and within 24 hours all the spores have produced germ tubes (pl. 12, figs. 6 and 7). The chromatophore elongates and passes into the germ tube, usually dividing during the process of migration (pl. 12, figs. 7, 8, and 9). The chromatophore is followed by the nucleus which at this time is in the early prophase of mitosis. Within 48 hours the chromatophores, the nucleus, and most of the cytoplasm have migrated into the germ tube which enlarges at the distal end (pl. 12, figs. 9–12). By the end of 72 hours the first transverse wall has been formed across the germ tube separating the enlarged tip from the rest of the tube (pl. 12, fig. 13). This leaves the old spore wall empty with the exception of a small remnant of cytoplasm which soon disintegrates. At this stage the one living cell contains one nucleus and two chromatophores. Occasionally, however, the nucleus divides before passing into the germ tube. In this case, one nucleus and two chromatophores pass into the enlarged distal end of the germ tube, the transverse wall separating the two nuclei is formed, leaving one nucleus with a small amount of cytoplasm in the tube, where it soon disintegrates and disappears.

The distal cell elongates and enlarges rapidly, the nucleus passes through mitosis for the first time and, as a result, a two-celled sporling is formed (pl. 12, figs. 13–18). The mitotic process here is similar to that found in the somatic mitosis of the sporophyte except that 13 chromosomes, the haploid number, are evident in the late prophase and metaphase (pl. 12, figs. 10, 14, and 16). The gametophytes continue to grow and within 16 days have formed monosiphonous filaments from 3 to 7 cells in length and measuring approximately 5μ in diameter (pl. 12, figs. 19–22). Within 26 days it is possible to distinguish the two kinds of plants. The larger or female gametophyte is made up of from 4 to 7 cells measuring 8 to 10μ in diameter, while the male gametophyte is more profuse in growth being made up of from 15 to 40 cells 4 to 5μ in diameter (pl. 13, figs. 2 and 3). In some cases the empty wall of the original spore is still clinging to the gametophyte but it never takes part in further growth. Sauvageau (1916c) found that in the closely related genus, *Alaria*, the embryospore (resting zoospore) retains a large amount of protoplasm after the first germ tube is formed and gives rise to a second germ tube. Thus he found that two gametophytes are usually produced from each embryospore.

Under favorable conditions the gametophytes reach maturity and begin to produce gametes in about 50 days after the germination of the zoospore. The male gametophytes form profusely branched clumps measuring approximately 1 mm. in diameter and bear single-celled antheridia in dense clusters at the tips of the branches (pl. 13, fig. 1). The female gametophytes, on the other hand, form clumps of approximately the same diameter but are made up of coarser filaments which branch sparsely. The tip cell of any branch may become transformed into an oogonium and the contents may form a single egg (pl. 13, fig. 4). At any one time a mature male gametophyte may bear hundreds of antheridia while the female gametophyte of corresponding age bears from two to twelve oogonia.

The length of time necessary for the maturation of the gametophytes depends largely upon the time of year at which they are grown. The zoospores placed in culture in April when the period of daylight is long matured in 7 weeks, those grown during the winter months (November to January) matured in from 12 to 16 weeks and those cultured in February required about 10 weeks to reach maturity.

The optimum temperature for the growth of the gametophytes is from 10° to 15° C, at which temperature they grow and reproduce readily, and continue to grow for a long period of time. At a temperature ranging from 15° to 20° C, growth is more rapid, gametangia are produced in abundance but few gametes are extruded, and the gametophytes do not live more than from six to eight weeks. At a lower temperature, from 5° to 10° C, growth is slow and very few reproductive organs are produced, but the plants may remain alive for months.

FORMATION OF THE ANTHERIDIUM AND ANTHEROZOID

The antheridia which form conspicuous clusters at the tips of the erect branches of the male gametophyte, are produced abundantly by the repeated divisions of the cells in the apical region. They are produced first from the apical cell of a branch in which, previous to division, the cytoplasm appears to grow denser and take the stain more readily. The nucleus then enlarges and passes through the typical mitotic process (pl. 11, figs. 2, 3, 4, 5, and 6). A transverse wall is laid down between the two daughter nuclei and the apical cell thus formed becomes the antheridium. Of the three to six chromatophores present in the apical cell of the branch, one, or occasionally two, passes into the antheridium as division takes place. The apical cell may divide several times in a similar fashion and produce a cluster of antheridia at the tip of the branch (pl. 13, figs. 1 and 1*a*). Later on any cell toward the tip of the branch may become an antheridium initial and, by the method of repeated division described above for the apical cell, may give rise to another cluster of antheridia (pl. 13, figs. 1*a* and 5). The production of antheridia is limited largely to the apical region of the branches and the cells of the main axis remain entirely sterile.

Soon after the antheridium is formed from the initial cell the contents round up and pull away from the wall as the apex becomes thickened or swollen in a manner similar to that found in the developing zoosporangium. The entire contents of the antheridium is used up in the formation of a single male gamete (pl. 13, fig. 5). The swollen tip eventually splits open forming a beak through which the mature antherozoid escapes. The male gamete as seen within the antheridium contains a nucleus, one or occasionally two chromatophores, a distinct red eyespot, and usually a large vacuole. The chromatophore gradually grows pale and less distinct in form until by the time the antherozoid is discharged it may appear as an indefinite brownish green mass at one side of the cell (pl. 13, figs. 6, 8, and 9). Ueda (1929) describes a similar situation in regard to the male gametes of *Laminaria religiosa* when he states that they are a pale yellowish green or almost colorless.

The antherozoid measures about 2.2 by 3.4μ and is pyriform in shape having the general appearance of a minute zoospore. There are two laterally placed cilia of unequal length, the longer one, which points in an anterior direction, is 6–7μ long. The shorter cilium, which usually points in a posterior direction, is evident only when the antherozoid is in motion and is approximately equal in length to the diameter of the antherozoid at the point of attachment, or about 2μ (pl. 13, fig. 7). The distinct red eyespot is associated with the pale remnant of the chromatophore and is situated close to the base of the cilia. The antherozoid swims in a fashion similar to that of the zoospore and in culture occasionally may be observed in the water in close proximity to the egg.

Since the gametophytes are microscopic in size and the process of liberation of the antherozoids must be watched through a microscope, it is only by chance that one is fortunate enough to observe fertilization as it takes place in the artificial cultures. It is only rarely possible to bring more than one apical cluster of antheridia into the field of vision of the microscope and usually not more than one antherozoid in a cluster is mature at any one time so that, even after many examinations have been made, the process of liberation of the antherozoids is rarely witnessed. The situation is made still more complex by the fact that often, especially in old cultures, small protozoans may be present which are very similar to the antherozoids in size, shape, and position of the cilia. In order to make certain of the identity of the antherozoids, one must actually see them liberated from the antheridium and follow them in their movements. This was done several times throughout the several weeks of close observation of the mature male gametophytes. The male gamete was seen to emerge slowly from the antheridium, remain attached at the apex for a time while the motion of the cilia was evident, and then swim rapidly away, soon passing out of the field of vision. In such preparation it is difficult to observe whether or not the antherozoids swim directly to the egg, since the pressure of the cover slip undoubtedly impedes them in their natural movements. Bodies having the appearance of antherozoids could be observed, however, in the neighborhood of the recently extruded egg and the process of fertilization was studied in similar preparations which were removed from the cultures, fixed, and stained at this time.

FORMATION OF THE OOGONIUM AND EGG

On the female gametophytes of the 50-day-old cultures erect branches are commonly found bearing large apical cells conspicuous on account of their dense contents. These cells elongate to about twice the length of the normal vegetative cells as the wall at the apex becomes swollen. The entire content of this cell pulls away from the wall, forming a long cylindrical body containing numerous chromatophores and a single large nucleus (pl. 13, fig. 4). At the apex of this oogonium the thickened wall splits, developing a beak through which the egg emerges (pl. 15, figs. 1 and 2). The egg rounds up as it emerges from the oogonium and usually remains in position at the tip, where it is fertilized. The oogonium contains, in addition to the egg, a small amount of highly vacuolated cytoplasm bearing a few chromatophores. This cytoplasmic mass is extruded with the egg and remains attached to the lower part of the egg, or in close proximity to it, for a long period before it disintegrates.

The unfertilized egg is a spherical or ovoid body surrounded by a delicate plasma membrane, it measures 18 to 25μ in diameter and contains one nucleus and many chromatophores, which are distributed irregularly throughout the cytoplasm. Although the egg usually remains at the mouth of the oogonium, it may be displaced and develop entirely away from the female gametophyte.

FERTILIZATION

In cultures containing mature male and female gametophytes the antherozoids can occasionally be seen clustered about the recently extruded eggs. One antherozoid enters and effects fertilization while the others round up, lose their cilia, and remain at the periphery of the egg for a short time before they disintegrate. Slides fixed and stained at this time show the antherozoids clustered near the egg, both of them surrounded by delicate plasma membranes (pl. 14, fig. 1). One antherozoid comes into contact with the egg, the adjacent plasma membranes become obscure, and the contents of the male gamete pass into the egg. At the point of entrance a small protuberance is left on the surface of the egg for a time, but is eventually absorbed and leveled down as the process of fertilization progresses (pl. 14, fig. 2). The position within the egg of both the male and female nuclei is very evident in the stained material but the fate of the cytoplasmic body of the antherozoid is difficult to determine. In his study on *Fucus,* Strasburger (1897) concluded that the cytoplasm of the antherozoid unites with the cytoplasm of the egg at the time of entrance. Yamanouchi (1912), however, in the egg of *Cutleria collaris* observed a clear area about the male nucleus as it migrated toward the nucleus of the egg, as though it was carrying with it some of its own cytoplasm. Since in the egg of *Pterygophora* there is no indication of the cytoplasm of the antherozoid around the male nucleus, it is likely that the cytoplasm of the two gametes is united as the antherozoid enters, and that only the nucleus of the male gamete migrates toward the egg nucleus. A distinct wall is developed around the egg soon after the male nucleus gains entrance (pl. 14, fig. 3). The male nucleus is in an early prophase condition when it enters the egg and as it migrates from the periphery of the egg toward the female nucleus, the chromatin granules enlarge while the nucleolus becomes less distinct (pl. 14, figs. 2, 3, and 5). As the male nucleus advances, the egg nucleus enlarges and passes through the early prophase stages of division. The male nucleus now becomes closely applied to that of the egg, the intervening nuclear membranes dissolve, the chromatin granules pass from the male nucleus into that of the female, and the nuclear membrane at the point of entrance is reformed. The nuclear material of the two gametes fuses and becomes indistinguishable one part from the other (pl. 14, figs. 4 and 5). The chromatin granules of the fusion nucleus become less distinct and for a time it appears to be in an early prophase condition. This conclusion is based on numerous observations of eggs with well developed walls, and therefore fertilized eggs, which contained a single large nucleus in the early prophase stage of division. The zygote nucleus passes through prophase into metaphase where the diploid number of chromosomes is again evident (pl. 14, figs. 4 and 8). The nuclei of the two daughter cells divide again, either simultaneously or successively, and as a result a three- or four-celled sporophyte is produced (pl. 14, fig. 9). Somatic mitosis proceeds in the characteristic fashion as was described for the mature sporophyte and the diploid number of chromosomes is again evident in each metaphase (pl. 14, figs. 6 and 9, and pl. 15, figs. 3, 4, and 5).

DEVELOPMENT OF THE SPOROPHYTE

In artificial cultures the fertilized egg usually remains in position at the neck of the oogonium where it develops into the young sporophyte. At first, cell division takes place in one plane only, resulting in a short thick monosiphonous filament of from eight to ten cells. Under conditions most favorable for growth this is produced in a period of about eight days. The cells in the apical region are the first to divide by a longitudinal septum, and are followed rapidly by the other cells of the filament with the exception of the basal cell, which becomes the rhizoid initial (pl. 15, fig. 6). Later, all cells divide rapidly in both planes forming a large flat monostromatic thallus (pl. 15, figs. 7, 8, and 9).

The rhizoid is formed in a manner comparable to that found in the production of root hairs from the epidermal cells of the roots in higher plants. A protuberance is formed from the rhizoid initial cell of the young sporophyte, and the nucleus, together with the four to six chromatophores contained in the original cell, passes into the swelling as it elongates (pl. 15, figs. 6 and 10). This process continues to take place from adjacent cells until a clump of rhizoids has been formed from the cells at the base of the sporophyte. The nucleus and chromatophores in the protuberance never divide, thus the rhizoids are practically colorless outgrowths with no cross-walls and no branches.

As growth in the sporophyte continues, the thallus becomes broad at the tip, forming a flat expanded blade which narrows sharply to a stipe-like region, at the base of which the rhizoids are borne (pl. 15, fig. 11). Soon the cells in the basal region divide in the third plane, producing a cylindrical stipe. When the sporophytes have reached approximately 3 mm. in length, the cells at the base of the blade also begin to divide in the third plane and give rise to a distromatic region. It was impossible to trace development beyond this point since, at this time, the temperature in the culture chamber was allowed to rise above the critical point and the death of the sporophytes resulted.

SUMMARY

1. The macroscopic plant or sporophyte generation of *Pterygophora californica* is diploid. A study of the somatic mitosis reveals a chromosome number of 26.

2. No spireme is evident in somatic mitosis, the chromosomes being formed by the fusion of the chromatin granules which become aggregated at the junction of the reticular fibrils.

3. The nucleus and chromosomes are exceedingly small and, on account of their minute size, little can be determined as to their morphology. Three pairs of short rods, one pair of very small spherical chromosomes, and nine pairs of ovoid choromosomes all measuring less than 1μ in length are distinguishable in the metaphase plate of somatic mitosis.

4. The reduction in chromosome number occurs in the first division of the zoosporangium nucleus. A distinct spireme, synizetic knot, and a typical diakinesis configuration are conspicuous features of reduction

division. The spireme is evident only in reduction division. The 13 bivalent chromosomes are present at the metaphase of reduction division and 13 univalent chromosomes are present at all subsequent nuclear divisions in the zoosporangium.

5. The haploid zoospores upon germination give rise to haploid gametophytes ($n=13$). The zoospores are homosporous and produce dioecious gametophytes.

6. The male and female gametophytes are alike in the early stages of development, but it is possible to distinguish the two by the marked difference in the diameter of the filaments by the time they are about three weeks old.

7. Under favorable conditions, the gametophytes mature in 50 days and continue to grow and fruit for several months.

8. The gametes are heterogamous. One large non-motile egg is borne in each oogonium and one minute motile antherozoid in each antheridium.

9. The male gamete measures 2.2 by 3.4μ, is pyriform in shape and laterally biciliate. It contains a nucleus, an eyespot, and a remnant of a chromatophore.

10. Fertilization occurs soon after the egg is discharged from the oogonium. Only one antherozoid enters, after which a wall is formed about the egg.

11. In the egg, the male and female nuclei fuse when in the early prophase of division. The 26 chromosomes become evident at metaphase in the fusion nucleus, which then passes through typical anaphase and telophase stages as the egg elongates, and finally a transverse wall is formed between the two daughter nuclei.

12. The diploid number of chromosomes is evident at the division of the nucleus in the young sporophytes grown in culture ($2n=26$).

13. In *Pterygophora californica* an alternation of generations has been demonstrated in which the diploid or sporophyte generation far exceeds the haploid or gametophytic generation both in size and organization, a situation which is common with all members of the Laminariales that have been studied by previous workers.

ACKNOWLEDGMENTS

In conclusion the writer wishes to express her appreciation to Professor N. L. Gardner for his helpful suggestions and criticisms during the work, and to Professor W. A. Setchell through whose kindness many facilities were afforded in the course of this investigation.

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EXPLANATION OF PLATES

PLATE 9—SOMATIC MITOSIS

Fig. 1. A cell from the inner cortex, containing a typical resting nucleus, five large vacuoles, and seven chromatophores. x 1500.

Fig. 2. A similar cell with the nucleus in a very early prophase stage; the nucleus has enlarged two to three times and a distinct reticulum has developed. x 1500.

Fig. 3. A cell with the nucleus in the prophase, showing a reticulum with clumps of chromatin at the junction of the fibrils. x 1500.

Fig. 4. A later prophase stage with distinct chromatin knots and a small pale nucleolus. x 1500.

Fig. 5. A metaphase plate showing the chromosomes in the process of splitting; no nuclear membrane present ($2n=26$). x 1500.

Fig. 6. Late prophase showing 26 chromosomes, some with fragments of the fibrils attached; nuclear membrane present. x 1500.

Fig. 7. Two nuclei in late prophase; nuclear membrane still present; transverse wall forming ($2n=26$). x 1500.

Fig. 8. Late anaphase; a membrane forming between the daughter nuclei; spindle fibers remaining in the vicinity of the clumps of chromosomes. x 1500.

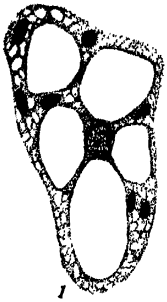
Fig. 9. Anaphase; spindle fibers vanishing in the central region. x 1500.

Fig. 10. Side view of an early anaphase plate, showing the distinct spindle fibers, centrosomes, centrospheres, and a few astral rays. x 2000.

Fig. 11. Telophase; chromosomes aggregated together and a new nuclear membrane developed; early stage in transverse septum formation. x 1500.

Fig. 12. A cell containing four nuclei, the upper two in prophase, the third in the resting condition, and the fourth in early prophase; no indication of transverse walls here. x 1500.

Fig. 13. Two transverse septums forming simultaneously, cutting an elogated three-nucleated cell into three parts. x 1500.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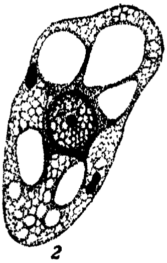
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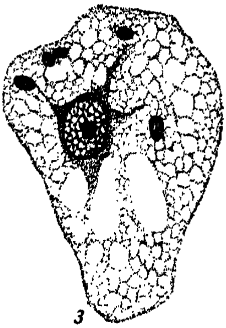
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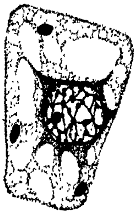
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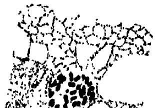
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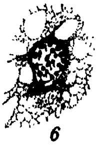
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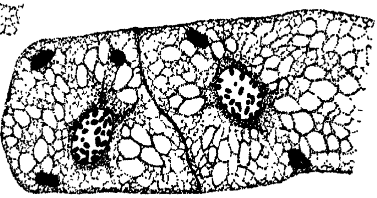
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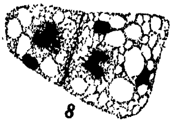
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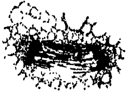
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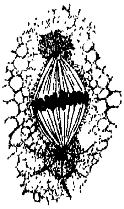
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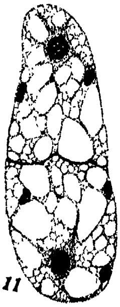
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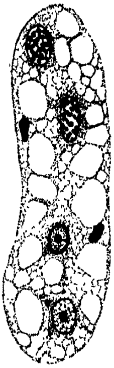
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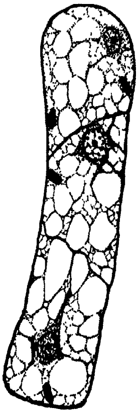
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PLATE 10—FORMATION OF THE ZOOSPORES

Fig. 1. Young zoosporangium initial, containing five chromatophores and a nucleus in the resting condition. x 1150.

Figs. 2, 3. Older zoosporangia initials with the nuclei in early prophase, showing the reticulum and clumps of chromatin. Figure 3 represents the more advanced stage showing larger chromatin knots. x 1150.

Fig. 4. An early stage in the formation of the spireme; the reticulum is transformed into several threads. x 1150.

Figs. 5, 6. Stages in synizesis. x 1150.

Figs. 7–8. The threads in the spireme breaking into segments in the process of formation of the bivalent chromosomes. x 1150.

Figs. 9, 10. Diakinesis, showing the 13 bivalent chromosomes. x 1150.

Figs. 11, 12. Polar views of metaphase, showing the 13 bivalent chromosomes; the nuclear membrane has disappeared. x 1150.

Fig. 13. A side view of metaphase showing the spindle and centrospheres. x 1150.

Fig. 14. Late prophase of second division showing 13 univalent chromosomes and a portion of the reticulum. x 1150.

Fig. 15. Anaphase of second division; spindle, centrosomes, and centrospheres present. x 1150.

Fig. 16. Late anaphase. x 1150.

Fig. 17. Late prophase of the third nuclear division. x 1150.

Fig. 18. Metaphase of the third nuclear division showing four metaphase plates of 13 chromosomes each. x 1540.

Fig. 19. Eight nuclei in the resting condition; the chromatophores having divided so that one is associated with each nucleus. x 1150.

Fig. 20. Prophase of the fourth nuclear division showing eight nuclei in the early prophase condition. x 1150.

Fig. 21. Sixteen nuclei in the resting condition; one chromatophore associated with each nucleus. x 1150.

Fig. 22. Early prophase of the fifth nuclear division showing 12 nuclei in the late prophase and one in metaphase. x 1150.

Figs. 23, 24. Sporangia containing nuclei in the fifth division showing typical prophase, metaphase, and anaphase stages. x 1150.

Fig. 25. Thirty-two nuclei in the resting stage previous to the formation of cleavage furrows; one chromatophore is associated with each nucleus. x 1150.

Fig. 26. A zoosporangium containing 32 zoospore primordia; cytoplasm pulled away from the wall, cleavage furrows formed between the nuclei, and a thick cap at the apex of the sporangium. Each primordium contains a nucleus and a chromatophore, and is surrounded by a plasma membrane. x 1150.

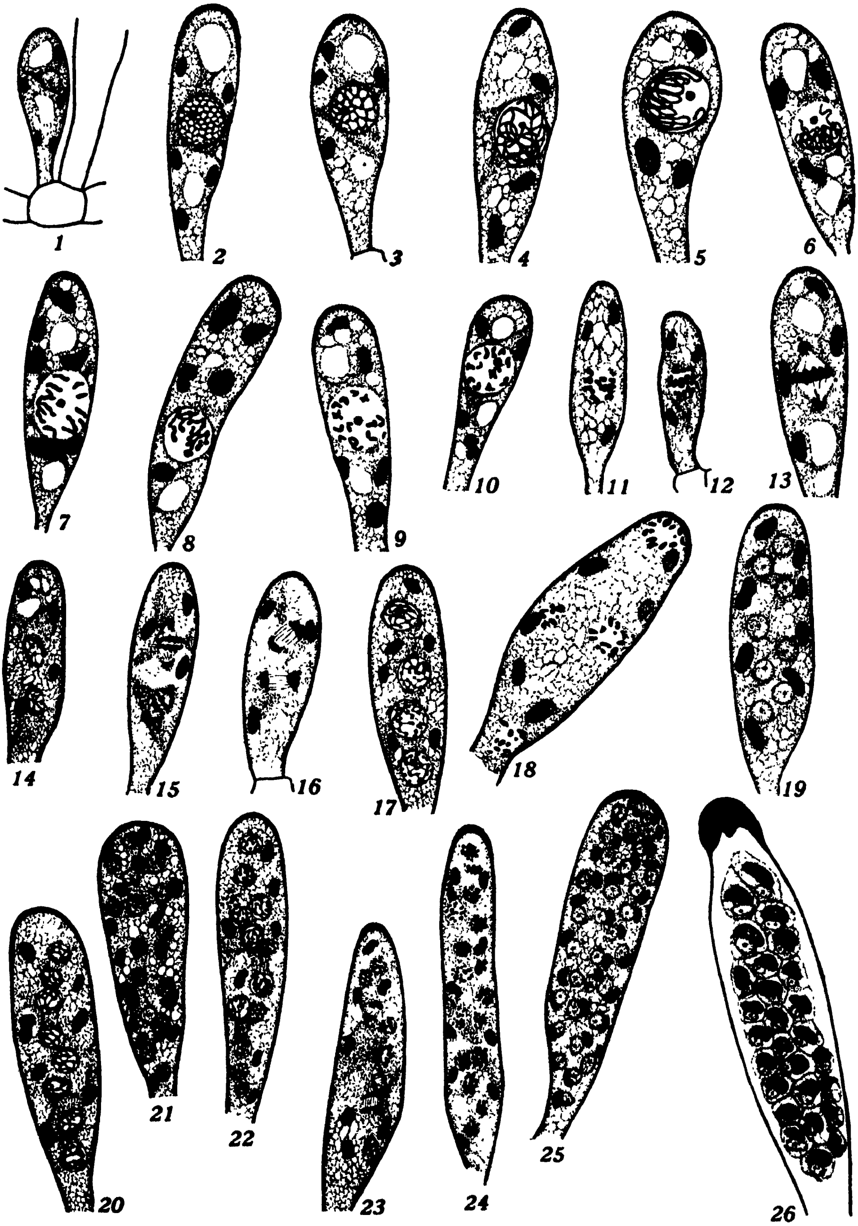


PLATE 11

GAMETANGIA INITIALS, CHROMOSOME FIGURES, AND ZOOSPORANGIA INITIALS

Fig. 1. An apical cell from the female gametophyte; the nucleus in anaphase with the haploid number of chromosomes. x 1500.

Fig. 2. Apical cell from a branch of the male gametophyte. x 1500.

Fig. 3. Anaphase of nuclear division in the apical cell of the male gametophyte showing the achromatic figure. x 1500.

Fig. 4. Late prophase in the apical cell of the male gametophyte. x 1500.

Fig. 5. Early anaphase showing the spindle and centrospheres. x 1500.

Fig. 6. Prophase in the apical cell of the male gametophyte. x 1500.

Fig. 7. A metaphase plate of somatic mitosis showing the three pairs of rod-shaped chromosomes, one pair of small spherical chromosomes, and nine pairs of oval shaped chromosomes ($2n=26$). x 2960.

Fig. 8. Diakinesis in the first division of the zoosporangium nucleus. x 3300.

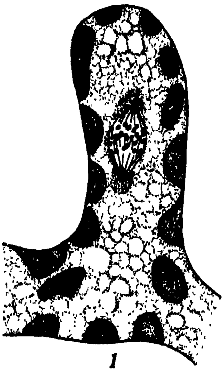
Fig. 9. Metaphase plate of the second nuclear division in the zoosporangium ($n=13$). x 2960.

Fig. 10. Metaphase plate of reduction division showing the 13 bivalent chromosomes. x 2960.

Fig. 11. A transverse section of the sorus showing the method of origin of the paraphyses and zoosporangia from the surface cells. x 1000.

Fig. 12. Metaphase plate in a surface cell previous to the formation of the paraphysis ($2n=26$). x 1500.

Fig. 13. Metaphase plate in a surface cell previous to the formation of the zoosporangium initial ($2n=26$). x 1500.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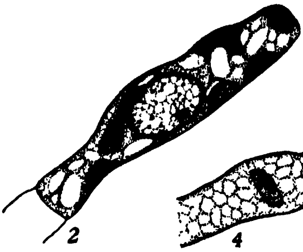
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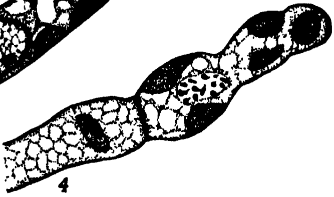
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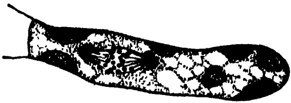
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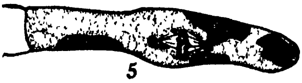
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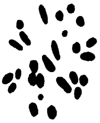
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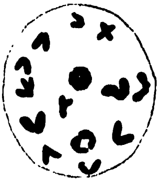
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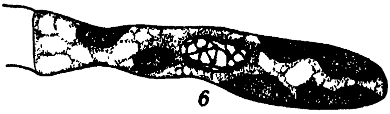
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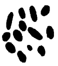
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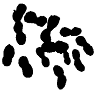
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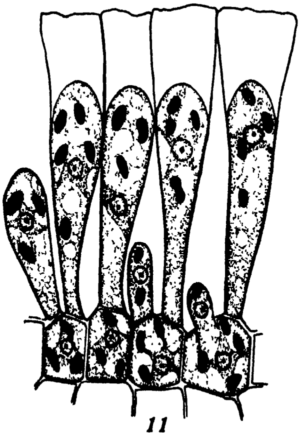
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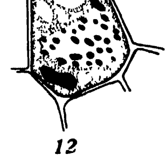
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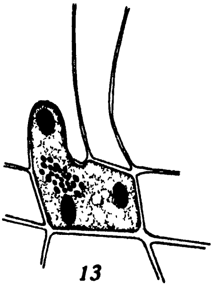
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PLATE 12—DEVELOPMENT OF THE GAMETOPHYTES

Fig. 1. Zoospores in the motile state, drawn from living material. x 750.

Fig. 2. Zoospore from living material showing two lateral cilia and a chromatophore with which is associated an eyespot. x 1500.

Figs. 3, 4. Zoospores attached to the slide and in the process of rounding up; drawn from stained material. x 1500.

Fig. 5. A spore attached to the slide from a 12-hour culture; a distinct wall is present. x 1500.

Fig. 6. A spore from a 16-hour culture showing the beginning of a germ tube. x 1500.

Figs. 7, 8. Sporlings from a 24-hour culture. x 1500.

Fig. 9. Sporling from a 4-day culture; the chromatophore has divided. x 1500.

Fig. 10. Metaphase plate drawn from a cell of the young gametophyte ($n=13$). x 2960.

Figs. 11, 12. Sporlings from a 5-day culture; most of the cell contents have migrated into the enlarged end of the germ tube. x 1500.

Fig. 13. A sporling from a 5-day culture showing the first transverse wall; the nucleus in the resting stage. x 1500.

Fig. 14. A sporling from a 5-day culture; the distal cell has enlarged and the nucleus is in the late prophase stage ($n=13$). x 1500.

Fig. 15. A sporling from a 10-day culture with the nucleus in early anaphase and the typical achromatic figure evident. x 1500.

Fig. 16. A sporling from a 10-day culture with the nucleus in metaphase ($n=13$). x 1500.

Fig. 17. A sporling from a 10-day culture with the nucleus in telophase. x 1500.

Fig. 18. A sporling from a 10-day culture: the second transverse wall has been formed. x 1500.

Figs. 19–22. Sporlings from a 16-day culture showing no differentiation between male and female gametophytes. x 750.

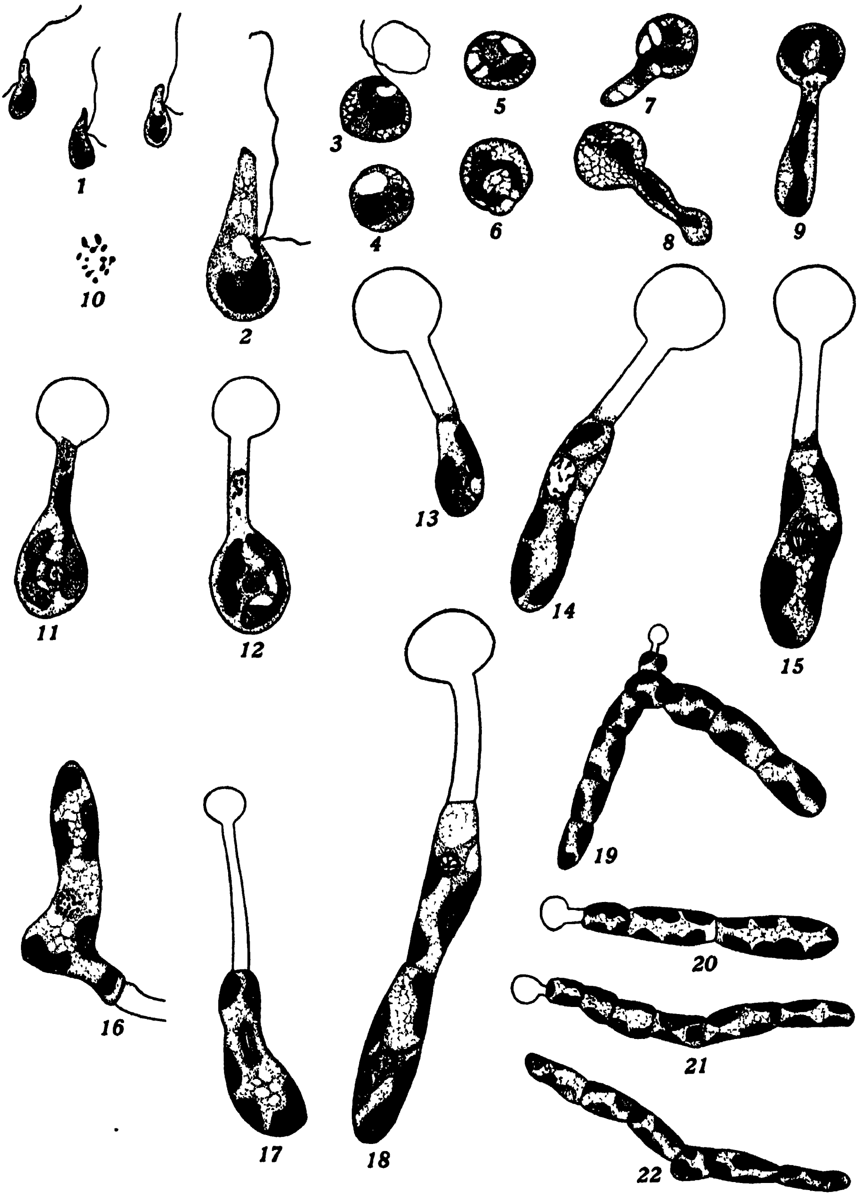


PLATE 13

THE MALE AND FEMALE GAMETOPHYTES

Fig. 1. A mature male gametophyte from a 53-day old culture with clusters of antheridia at the tips of the branches. x 380.

Fig. 1*a*. The process of formation of the antheridia from the apical cell of a branch of the male gametophyte. The upper cell shows an antheridium before the differentiation of the antherozoid, and the lower a step in the process of formation of an antheridium from the mother cell. x 1540.

Fig. 2. A male gametophyte from a 34-day old culture. x 540.

Fig. 3. A female gametophyte from a 34-day old culture. x 540.

Fig. 4. A mature female gametophyte from a 53-day old culture; showing at the left an egg enclosed in the oogonium, next toward the right an egg recently extruded, next a three-celled sporophyte at the tip of the oogonium, and at the extreme right a spherical unfertilized egg. x 380.

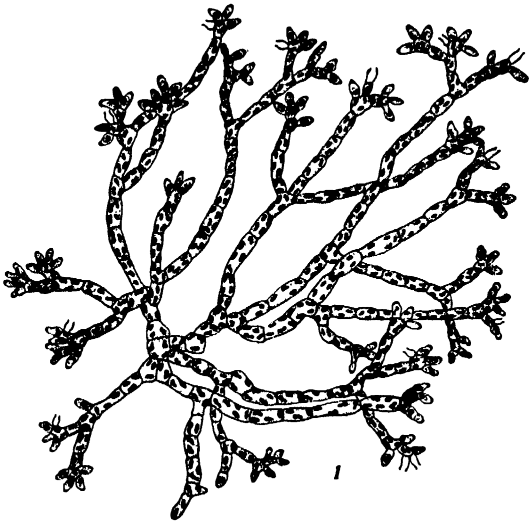
Fig. 5. The tip of a male branch showing an antheridial cluster. Antheridia with thickened caps, each containing a single male gamete are shown; also two empty antheridia as they appear after the discharge of the antherozoids. x 1150.

Fig. 6. A male gamete resting on the tip of the antheridium from which it has recently been discharged. x 1540.

Fig. 7. An antherozoid drawn from living material, showing two cilia, an eyespot associated with the chromatophore near the point of attachment of the cilia, and the remnants of two chromatophores. x 1540.

Fig. 8. An antherozoid drawn from stained material showing the large nucleus in a resting condition. x 1540.

Fig. 9. An antherozoid contained in an antheridium as seen in living material. A small chromatophore, an eyespot, and a large vacuole are evident. x 1540.



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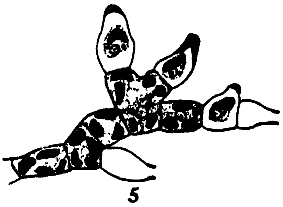

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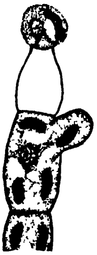

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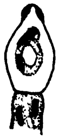

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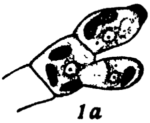

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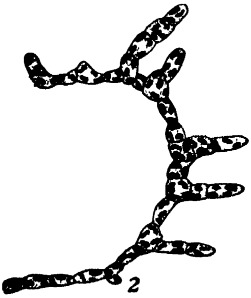

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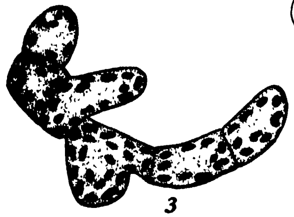

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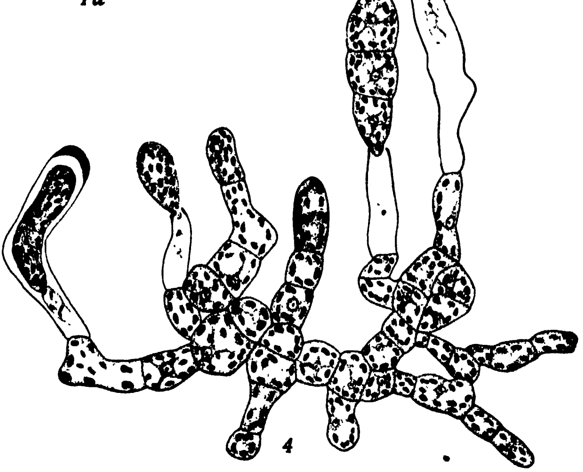

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PLATE 14—FERTILIZATION

Fig. 1. An unfertilized egg enclosed in a plasma membrane, containing a nucleus in a very early prophase stage and many chromatophores; two male gametes in close proximity, one in a motile condition and the other rounded up and having a large nucleus in prophase. x 1500.

Fig. 2. The entrance of the male gamete through the plasma membrane of the egg. The body of the antherozoid forms a clear-appearing projection on the surface of the egg as the male and female nuclei draw together. x 1500.

Fig. 3. The egg after the male gamete has entered, showing the distinct thin wall which is produced around the egg after the entrance of the male gamete: both the nuclei in the prophase condition and lying close together. x 1500.

Fig. 4. An egg with the fusion nucleus in an early prophase condition. x 1500.

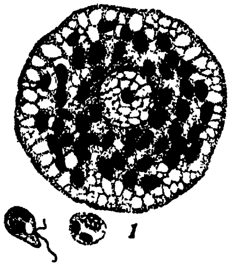
Fig. 5. The process of fusion showing the chromatin material from the male nucleus passing over into the female nucleus. x 1500.

Fig. 6. A metaphase plate of second division of the zygote nucleus ($2n=26$). x 2960.

Fig. 7. Side view of an early anaphase in the first division of the fusion nucleus showing the spindle, centrosomes and centrospheres. x 1500.

Fig. 8. Polar view of the first metaphase of the fusion nucleus ($2n=26$). x 1500.

Fig. 9. A three-celled sporophyte produced by two divisions of the fertilized egg, the upper cell containing a nucleus in telophase, the middle cell with a resting nucleus, and the lower one with two nuclei in metaphase ($2n=26$). x 1500.



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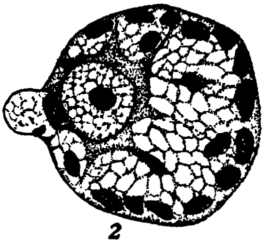

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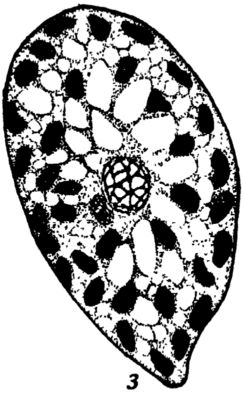

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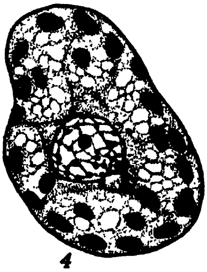

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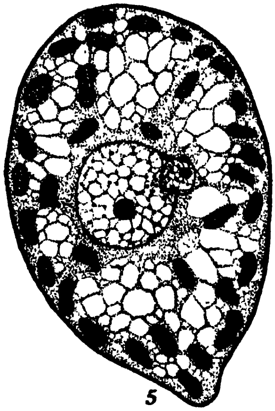

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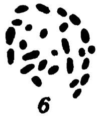

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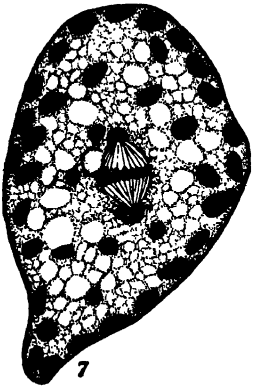

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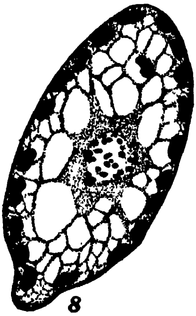

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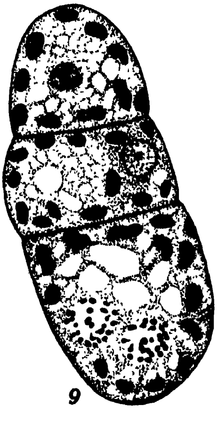

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PLATE 15

PRODUCTION OF THE FEMALE GAMETE AND THE DEVELOPMENT OF THE YOUNG SPOROPHYTE

Fig. 1. An egg in the process of extrusion from the oogonium. x 1000.

Fig. 2. An egg recently extruded from the oogonium showing the remnant of cytoplasm which in addition to the egg, is contained in oogonium. x 1000.

Fig. 3. A two-celled sporophyte at the neck of the oogonium: the two nuclei in metaphase of second division ($2n=26$). x 1000.

Fig. 4. A four-celled sporophyte. x 1000.

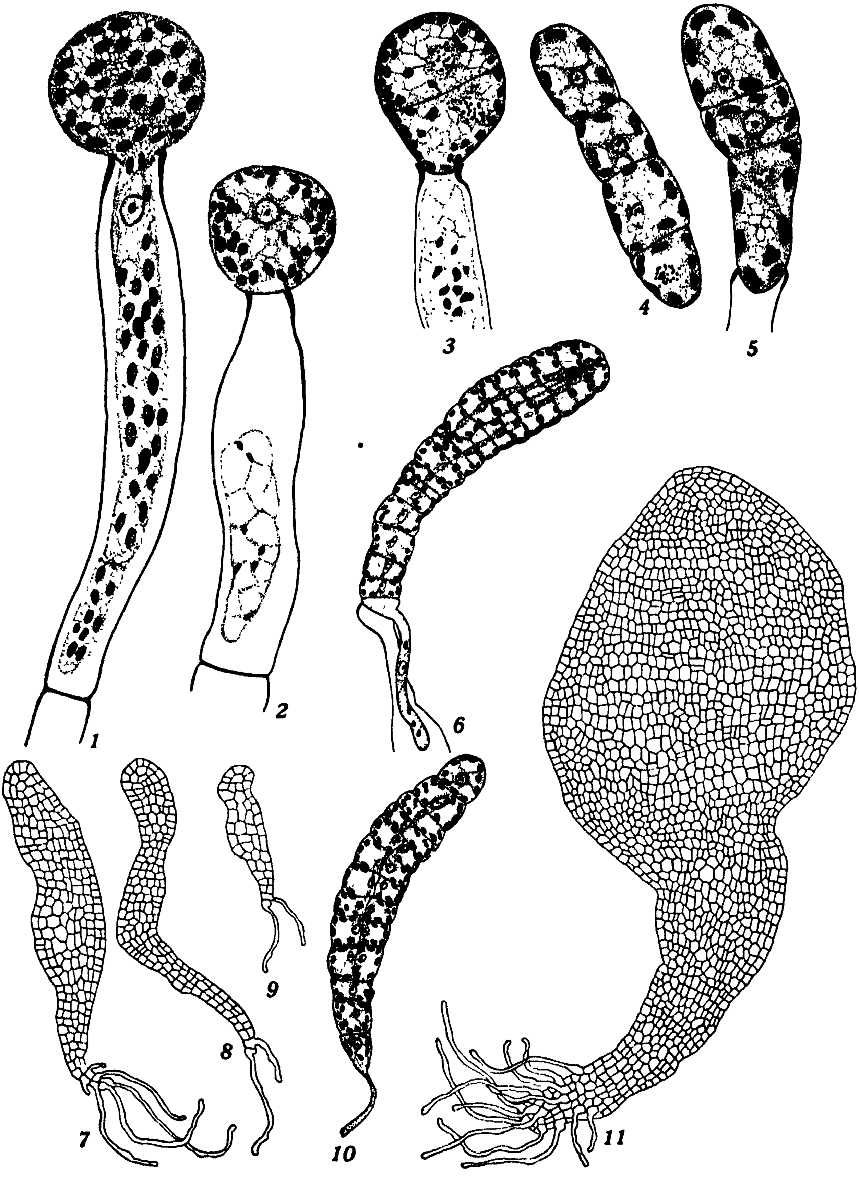
Fig. 5. A three-celled sporophyte resting on the old oogonium. x 1000.

Fig. 6. A young sporophyte resting on the tip of the old oogonium: the first longitudinal wall formed through the apical cells: the basal cell producing a single rhizoid which contains the nucleus and chromatophores from this cell. x 380.

Figs. 7–9. Young sporophytes of various ages, showing the production of a flat thallus from the monosiphonous filament. x 85.

Fig. 10. A young sporophyte showing the first longtitudinal walls in the subapical cells and a rhizoid produced from the basal cell.

Fig. 11. An older sporophyte differentiated to some extent into stipe and blade. The lower portion of the blade is distromatic and the stipe is polystromatic. x 85.



PANDANACEAE OF TAHITI

BY

UGLINO MARTELLI

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UGLINO MARTELLI

The Society Archipelago is formed of fourteen islands, of which some are very small. Their names are: Huaheine, Raiatea, Tahaa, Bora-Bora, Tubai, Marua, Mopiha, Bellingshausen, Fenuaura or Scilly, the Windward group; and Maitea, Tahiti, Tetiaroa, Moorea, Tapaimanu, the Leeward group. Except Mopiha, Bellingshausen, Tetiaroa, and Fenuaura, which are coral atolls, these islands are volcanic.

As regards their botanical aspect, it is commonly considered that the flora of this archipelago is one of the best known among those of Australasia; but I do not think it correct to consider it in this way, because if it is true that many botanists are well acquainted with Tahiti's flora, the same cannot be said of the thirteen other islands that comprise the whole Society group, whose names never, or very rarely, are reported on herbarium specimens or in the different oceanic floras. For instance, we know that the natives of Raiatea distinguish with different names the eight varieties of *Pandanus* that they use for weaving mats, baskets, or hats, but we cannot state whether this distinction is botanically correct and whether these varieties or microspecies are different from those of Tahiti.

From Tahiti two species of *Freycinetia* are known, *Fr. Victoriperrea* and a *Fr. sp.* that I have not yet described because it has been impossible for me to do so from the only sterile specimen I obtained from Tahiti in 1904, collected by Mr. MacFarlane, with the indication only of "smoking Pandanus." Are those two species of *Freycinetia* confined to Tahiti or do they live also on other volcanic islands of the archipelago? Does any *Freycinetia* live on the other thirteen islands of the group? I presume the existence of a *Freycinctia* on the heights of Raiatea, according to what Huguenin says in his book, Rajatea la Sacrée,

Sur les sommets où l'altitude tempère un peu la chaleur torride et où les nuages se trainent fréquemment, il se dépose, le soir et le matin, une très forte rosée qui entretient une végétation plus nourrie qu'à mi-côte et la marche au travers d'une

> brousse qui dépasse même la tête des chevaux, devient très difficile et très lente. Il faut toute une escorte d'indigènes armés de hâches et de longs couteaux pour se frayer un chemin et la vie est presque nulle tant on est enfoui dans des buisson touffus, semblables à des buis gigantesques. Les Pandanus nains sont nombre là-haut et leurs racines adventives trompeuses; elles se cassent sous le pied qui essaie de les escalades (p. 22).

This short description seems to me much more appropriate to a *Freycinetia* than to a *Pandanus,* but I cannot be certain. What I presume for Raiatea may equally be true of the other islands of the group, not only for Pandanaceae but also for all other plants of that flora. We may therefore conclude that while the flora of Tahiti is almost completely known, this is not true for the remaining islands of the archipelago. Nadeaud (Énumération des plantes indigènes de l'Ile de Tahiti, 1873) enumerates only one *Pandanus* (*odoratissimus,* the "Fara" of the natives) and one *Freycinetia (demissa = Victoriperrea);* in my Enumerazione delle Pandanaceae (Webbia, vol. 4, parte IIa, 1910–1913), I mentioned only three *Pandanus* and two *Freycinetia* from Tahiti. To the flora of this island belongs also the form called by Solander, *Pandanus tectorius,* about which I have previously published a note (Pandanus tectorius o Pandanus odoratissimus?, Nuovo Giornale Botanico Italiano, 1929).

Among the collection I have received for revision from Tahiti, I find some forms or microspecies of *Pandanus odoratissimus* not yet indicated as occurring there. Some of these are, I think, not indigenous in Tahiti, but introduced there recently from neighboring groups.

I give here an enumeration of the Tahitian Pandanaceae known up to the present time.

Freycinetia Gaud.

Freycinetia Victoriperrea Solms Laub., *in* Linnaea, 1878, p. 103.

An old specimen from Tahiti is in the Paris Herbarium. It is a specimen with leaves and one syncarp in a poor state of preservation. On a label is written: "Genre consacré à M. l'Amiral Duperré—Par M. Hombron, Voy. de l'Astrolabe et la Zélée, tab. . . . ."; on another strip of paper: "M. Morenhout"; and last, on a third bit of paper: "Freycinetia," with the name "Hombron" half torn off. These labels are very interesting as showing the history of this plant. "*Victoriperrea impavida*" is the name given to it by Gaudichaud in Dumont d'Urville, Voy. au Pôle sud et dans l'Océanie sur l'Astrolabe et la Zélée, Bot., p. 111, tab. 1; the plant was so named in honor of Victor Duperré, a French admiral. From the second label we know that the specimen was sent by Moerenhout,[1] probably in 1834, after the death of Dr. Bertero.

Freycinetia sp. **in Herb. Martelli, *legit* MacFarlane, 1904.**

This specimen was received from Tahiti in 1904 from Mr. MacFarlane; unfortunately it is a sterile plant and I have never been able to describe it. It has narrow leaves and looks a little like *Freycinetia Hombronii* of Samoa, but it seems to me to be different. I hope to receive in future complete specimens. Among the collections I recently received from Tahiti, I have not found this species.

PANDANUS

(Type of *Pandanus odoratissimum* Linn.)

Pandanus Menziesii **Gaud., *in* Bonite, tab. 1, fig. 14.**

Plate 16, figures 1, 2

Habitat.—Near the seashore on Harrison Smith's property, Papeari, August 30, 1929. Gerrit P. Wilder, no. 3 *(pro parte).*

Notes.—Under the same no. 3 of Wilder's collection and in the same packet, there were mixed together some phalanges of *Pandanus MacFarlanei,* some of *P. tessellatus,* and three that I think belong to *P. Menziesii* Gaud., since they seem to be very similar. Of this species, however, we do not know the native country. The types in the Paris collections were collected by Gaudichaud, not at Tahiti nor in any other island of the Society group, because "La Bonite" during its journey did not land there. I think that Gaudichaud probably gathered these phalanges at Hawaii. It is possible that *Pandanus Menziesii,* collected now at Tahiti, is an imported and cultivated plant.

Pandanus Drolletianus **Mart., *in* Webbia, 2:426 et 3, tav. 3, figs. 6–8.**

Pandanus MacFarlanei **Mart., *in* Webbia, 2:426, tav. 2, figs. 5–7.**

Syncarpia cernua, 33–23 cm. diam., oblongo-ovata, numerosissimis phalangibus instructis, phalanges, in toto, cuneatae sed potius e medio usque ad basim angustam sensim attenuatae, in dimidiam superiorem partem liberae sub-rectangulares vix convexae, faciebus latis, secundum loculos, parum canaliculatis, vertice planae, cum 8–9 interdum 10 lo-

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[1] A Dutchman, and consul of the United States in Oceania. He was a friend of Dr. C. Bertero, an Italian, and they put together in 1831–1832 a very rich herbarium of plants collected in Tahiti. Bertero left the island in April, 1832, and has not been heard of since. M. Moerenhout, in 1834, sent a numerous collection of plants from Tahiti to M. Orbigny in Paris (see Guillemin, Zephyrites taitensis, Ann. Sci. d'hist. nat., 1836–1837; Martelli, L'Arcipelago della Società e le sue Pandanaceae, *Memorie,* Soc. Sci. Nat. Pisa, 1932).

culis subaequalibus, latiusculis subconvexo-planis, a sulcis angustis profundis separatis. Stigmata lata, crassa, prominentia. Endocarpium in dimidiam superiorem partem phalangis locatum, 3 cm. spissum, superne rotundato-fimbriatum, inferne subrotundato-planum.

Habitat.—Tahiti, near the seashore, on Harrison Smith's property at Papeari; *legit* Gerrit P. Wilder, August 30, 1929, no. 3 *(pro parte)* in the herbarium of the University of California. Near Papawa Harbor (a single large tree), June 16, 1932, *legit* Setchell and Parks, no. 366 [see Setchell, Univ. Calif. Publ. Bot., **12**:146, 1926, sub. *P. tahitensis.*—W. A. S.].

Notes.—The specimens sent to me are noted with the number 3, but in the same parcel I found mixed three different species of Pandanus. Some phalanges belong to *Pandanus tessellatus* Mart., others to *P. Menziesii* Gaud., and others again to *P. MacFarlanei* Mart. In the parcel there is also a very beautiful photograph of a syncarp (see pl. 17).

Pandanus tahitensis **Mart., *in* Martelli, Pandanus Nove Specie, Webbia, 2, 1907: 428 et 4, parte Ia, tav. 7, fig. 1–3.**

Pandanus prismaticus Mart.

Plate 18

Syncarpium cernuum, solitarium, globoso-oblongum, 20–25 cm. circiter diam., a numerosis phalangibus, in parte libera inter se divaricatis, instructum. Phalanges 6 cm. longae, in dimidia superiore parte prismaticae, liberae, cubum simulantes, acute angulosae, ibique circiter 3 cm. diam.; lateribus latis, subplanis vel canaliculatis, interdum, secundum suturam loculorum, sulco angustissimo notatis; in dimidia inferiori parte connatae, fibroso-compactae, subabrupte attenuatae et in basim acutissimam desinentes, supra planae vel vix convexae, loculis 8–10, mediocribus vel parvulis, brevibus, convexo-pyramidatis, a sulcis superficialibus latiusculis separatis; sulcis a linea suberosa circumscriptis; stigmata mediocra, superantia. Endocarpium osseum in medio phalangis locatum, ambitu, in toto, rotundatum, 2–2.5 cm. spissum, in sectione longitudinali, supra, rotundato-vix pyramidatum, subfimbriatum, inferne rotundatum; mesocarpium superum 5–8 mm. spissum, cavernis parvis, spongioso-fibrosis; mesocarpium inferum ultra 2 cm. spissum, fibroso-subcompactum.

Habitat.—In Tahiti, near the seashore, on Harrison Smith's property at Papeari; *legit* Gerrit P. Wilder, no. 2, August 30, 1929.

Notes.—The shape of the free portion of the phalanges is characteristic. They look like cubes, although it is not really so. The pericarp is smooth, bright, and under a glass is minutely punctate. The phalanges which I keep in my herbarium have their inferior and connated part similar to a reversed and very acute cone.

Pandanus distinctus Mart.

Plates 19, 20

Syncarpium fere globosum 14–16 cm. diam. pluribus phalangibus instructum; phalangibus in parte superiore libera inter se divaricatis, in dimidia, adhaerentibus et in basilare late distinctis. Phalanges 5.5 cm. longae, in toto ambitu, turbinaeformes, raro compressae, acutissimae, penta-hexagonae, nasi contractae-angustatae, quasi caudatae vel pedunculatae, distinctae, haud fibrosae, deinsuper, usque fere ad apicem, sensim expansae et convexo-rotundatae, 3–4 cm. diam., e dimidio ad verticem, laeves et, in sicco, subnitidae; vertice explanatae, pluriloculares, loculis 5–7, interdum 8, parvis et laevibus, convexo-angulosis, a sulco angusto manifesto, sed parum profundo, separatis. Stigmata ± lata, prominentia. Endocarpium osseum in dimidia parte phalangis situm, fere 2.5 cm. spissum, ambitu utriunque plavum, supra ambitu sinuoso-pyramidatum, subtus sinuoso-fimbriatum. Mesocarpium superum cum cavernis fere subaequalibus, circiter 1 cm., inferum fibrosum compactum.

Habitat.—Tahiti, at Papeari near the seashore on Harrison Smith's property; *legit* Gerrit P. Wilder, no. 5; in Colonel Clay's yard, Papara; Gerrit P. Wilder, no. 6, August 1929.

Notes.—I have called this species "*distinctus*" for the reason that the phalanges are separated from one another in their lower parts. This character, however, is not peculiar to this species, since I have observed it also in other species.

Pandanus papeariensis Mart..

Plate 21

Syncarpium subglobosum, circiter 13 cm. diam., pluribus phalangibus confertis instructum; pedunculo breve 1.5 cm. crasso et in sicco longitudinaliter creberrime ruguloso. Phalanges turbinato-elongatae, circiter 5 cm., et 2–2.5 cm. diam. basin-versus sensim attenuatae quasi in cauda angusta (7 mm. crassa) protractae, acute penta-hexagonae, circiter e medio ad basim connatae, haud fibrosae, lateribus inaequalibus latis plano-subconvexis, interdum vix longitudinaliter concavo-canaliculatis, apice phalangium vix convexo, subplano; loculis paucis (4–5) parvis, brevibus, paullo convexis irregularibus a sulcis angustis haud profundis separatis, a stigmate papillaeformi prominulo superatis. Endocarpium osseum in medio phalangis situm, circiter 2 cent. spissum, in sectione longitudinali superne plus minusve profunde et late fimbriatum, in toto subplanum inferne plano-subconcavum. Mesocarpium inferum compactofibrosum, superum lacunosum spongioso-fibrosum.

Habitat.—Tahiti, near the seashore on Harrison Smith's property at Papeari; *legit* Gerrit P. Wilder, no. 1, September 2, 1929·

Notes.—Some years ago I had the opportunity of studying, in the collections of the University of Vienna, this new species, without being

able then to determine its native land. On the label was written only "Novara Expedition." For this reason I left the species undescribed. This specimen was collected during the journey of the Austrian frigate "Novara" (Reise der Oesterreichischen Fregatte Novara um die Erde in den Jahren 1857–1859 unter den Befehlen des Commodore B. von Wiillerstorf Urbair Wien. Triest, 1870).

During the progress of the present revision of the *Pandanus* of Tahiti, among the species collected by Mr. Wilder I have met this species of the "Novara" expedition. I suppose now, and with seemingly good reason, that the specimen of the University of Vienna may have been collected at Tahiti when it was visited by the frigate "Novara"[2] on its return voyage.

Pandanus odoratissimus var. *savaiensis* Mart., *in* Reichinger, Bot. u. Zool. Ergeb. v. Samoa, Neu-Guin. u. Salomon Ins., p. 5, fig. 5; Martelli, *in* Webbia, 4, parte IIa, tav. 9, figs. 4–7.

Habitat.—Tahiti. Shoot of cultivated plant, used for mats, hats, etc., said never to fruit. Yard of Dr. Williams' home at Mateiea; *legit* Gerrit P. Wilder, no. 8.

Leaves without smooth margins.

The same species has been collected in Samoa.

Among the Pandanus collection of Mr. Wilder there is another species noted with the "no. 7," but on account of its incompleteness I am unable to establish its specific position. On the label it says: "Single tree in Mr. Brander's yard, near Papeete, now cut down. Leaves used for cigarette papers. Aug. 1929. Phalanges all fallen."—Gerrit P. Wilder.

(Type of *Pandanus pedunculatus* R. Br.)

Pandanus tessellatus Mart.

Plate 16, figures 3–7

Phalanges 4.5 cm. longae, turbinatae in basi angustissima protractae, ambitu convexo-rotundatae, supra medium 2.5–3 cm. diam. ibique inter se liberae acute-pentagonae, lateribus inaequalibus, latis, planis vel vix concavis, laeves in sicco subnitidae, in dimidiam inferiorem partem connatae, fibroso-sericeae, vertice explanatae vel vix convexae, loculis 7–9 interdum 5–6, confertis vertice repletentibus, loculis, parvis, elevatis, pyramidatis acute angulosis basi latiusculis a sulcis angustis, profundis separatis; stigma in vertice loculorum promines, latum, subhorizontale, hippocrepicum, interdum cum superficie stigmatica subverticali, parte dorsali in disco subrectangulare, nitido protracta. Endocarpium, in sectione longitudinale, in dimidia parte phalangis situm 2 cm. spissum, ambitu subrotundatum sed inferne subexplanatum. Mesocarpium superum cum cavernis subaequalibus medulloso-fibrosis, mediocribus, inferum fibrosum.

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[2] The frigate "Novara," during its journey round the world (1857–1859) landed at Gibralta, Madeira, Rio de Janeiro, Cape of Good Hope, St. Pail Island, Amsterdam Island, Ceylon, Madras, Nicobar Island, Singapore, Java, Manila, Hong Kong, Shanghai, Puynipet or Ponape Island (Caroline), Sikayana Island (Solomon group), Sidney, Auckland, Tahiti, Valparaiso, Cape Horn, Gibraltar, Triest.

Habitat.—Tahiti, near the seashore on Harrison Smith's property, Papeari; *legit* Gerrit P. Wilder, no. 3, August 30, 1929.

These phalanges I found mixed in the same parcel noted no. 3 (Wilder) containing others belonging to *Pandanus Menziesii* and *P. MacFarlanei.*

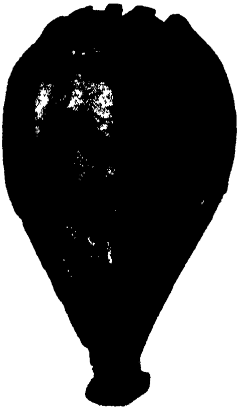
I think this Pandanus does not belong to the type of *odoratissimus* but rather to that of *Pandanus pedunculatus* R. Br. of Australia. Some time ago I received from Dr. C. T. White of Brisbane some phalanges collected at the northeast coast of East Australia (islands of the Capricorn group), which are similar to those of this species of Tahiti. They are very characteristic in the small locules and the very thick and acute pyramids at the top of the phalanges. A form of this same *Pandanus tessellatus* has also been collected at Rarotonga Island.

Pisa (Italy). From the Botanical Garden of the University, June, 1932.

EXPLANATION OF PLATES

PLATE 16

Figs. 1, 2. *Pandanus Menziesii* Gaud.
Figs. 3–7. *Pandanus tessellatus* Martelli



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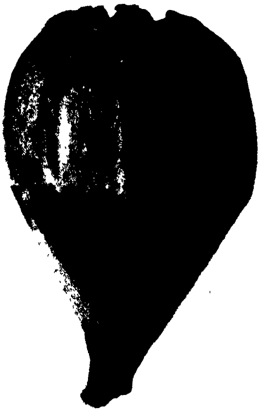

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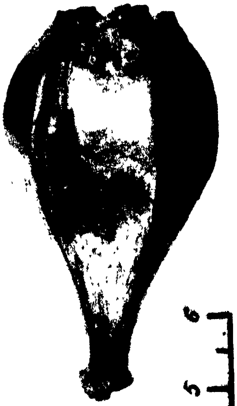

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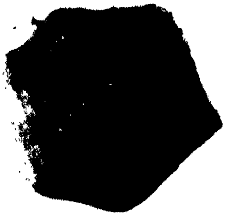

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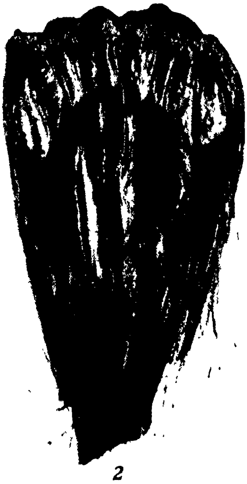

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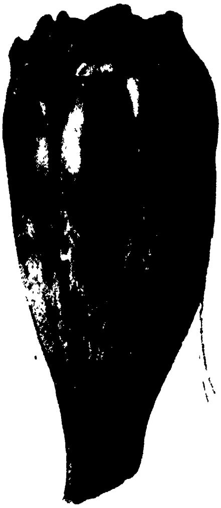

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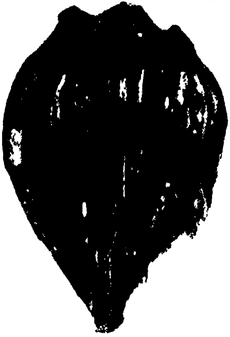

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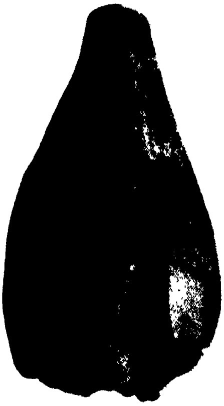
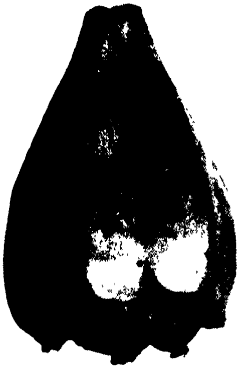
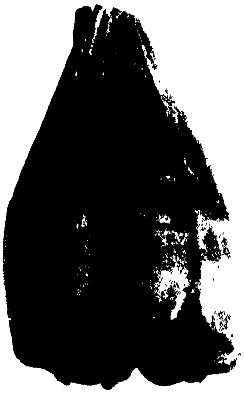
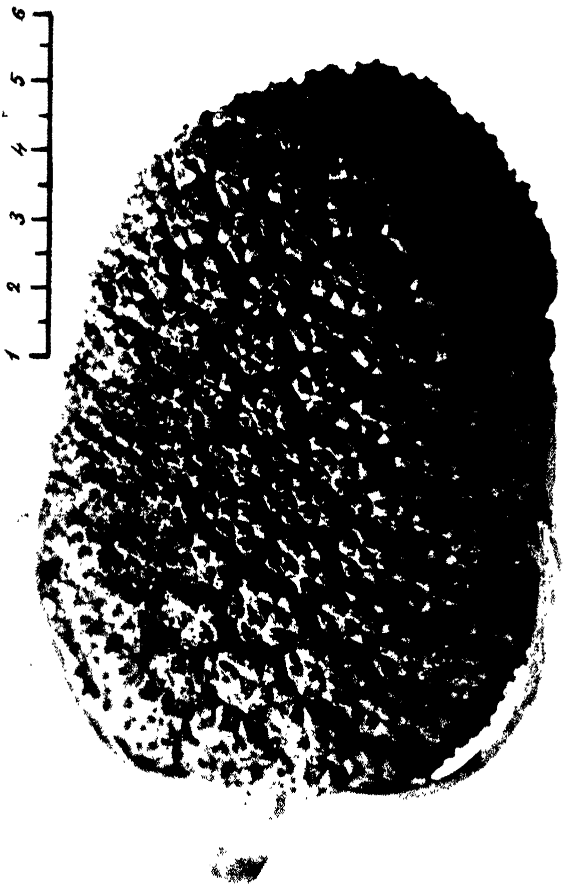
PLATE 17

Pandanus MacFarlanei Martelli





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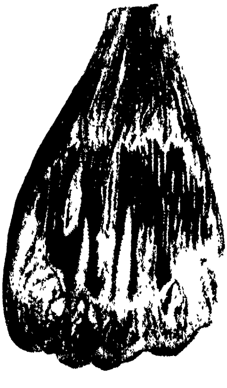

PLATE 18

Pandanus prismaticus Martelli

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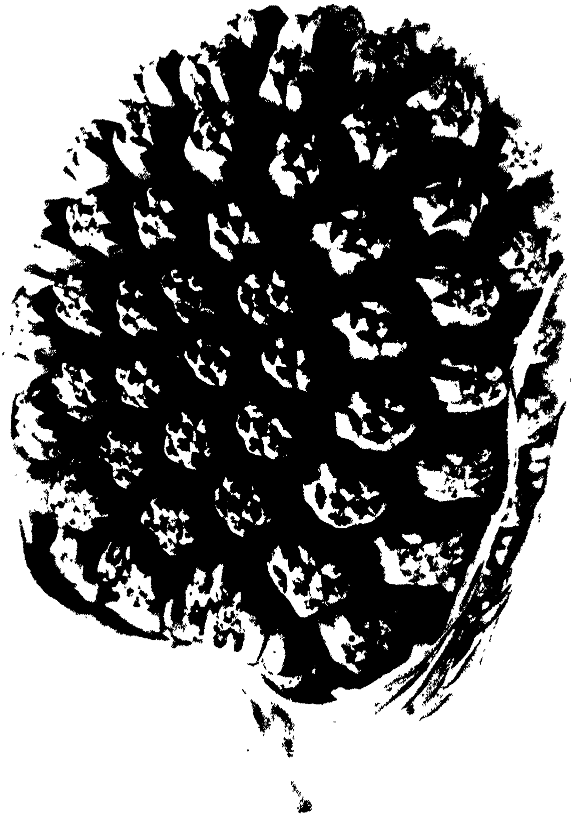

PLATE 19

Pandanus distinctus Martelli

PLATE 20

Pandanus distinctus Martelli

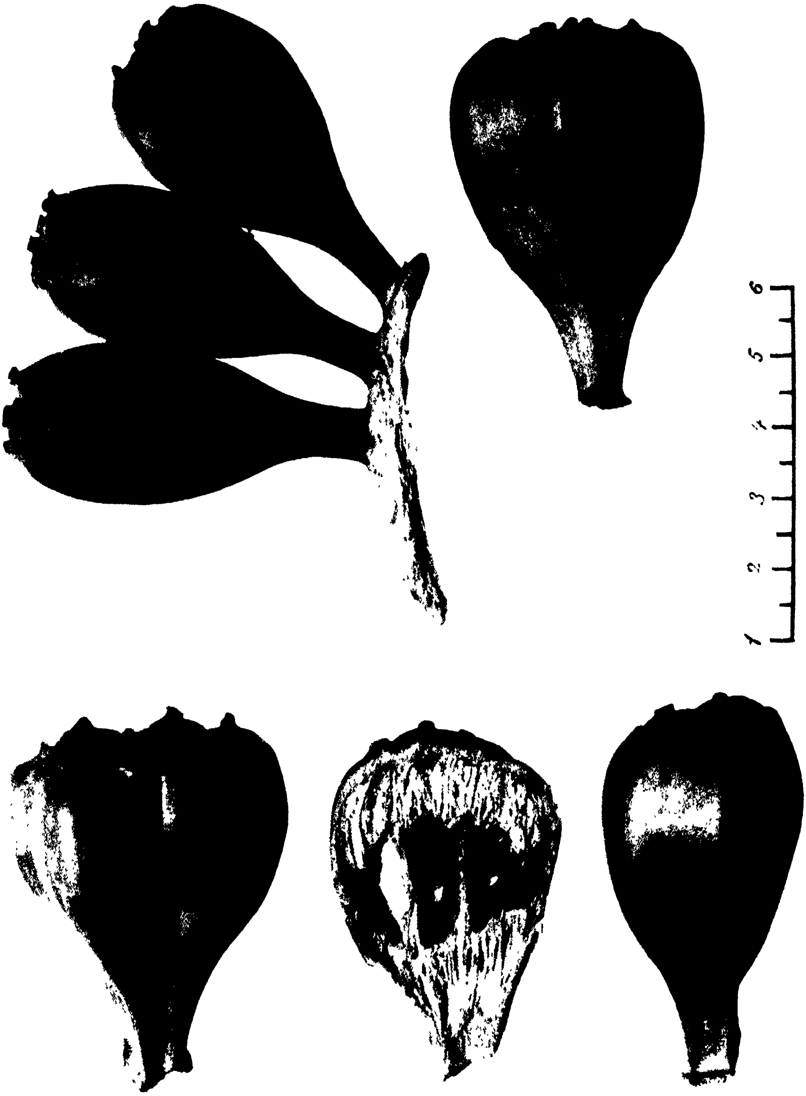
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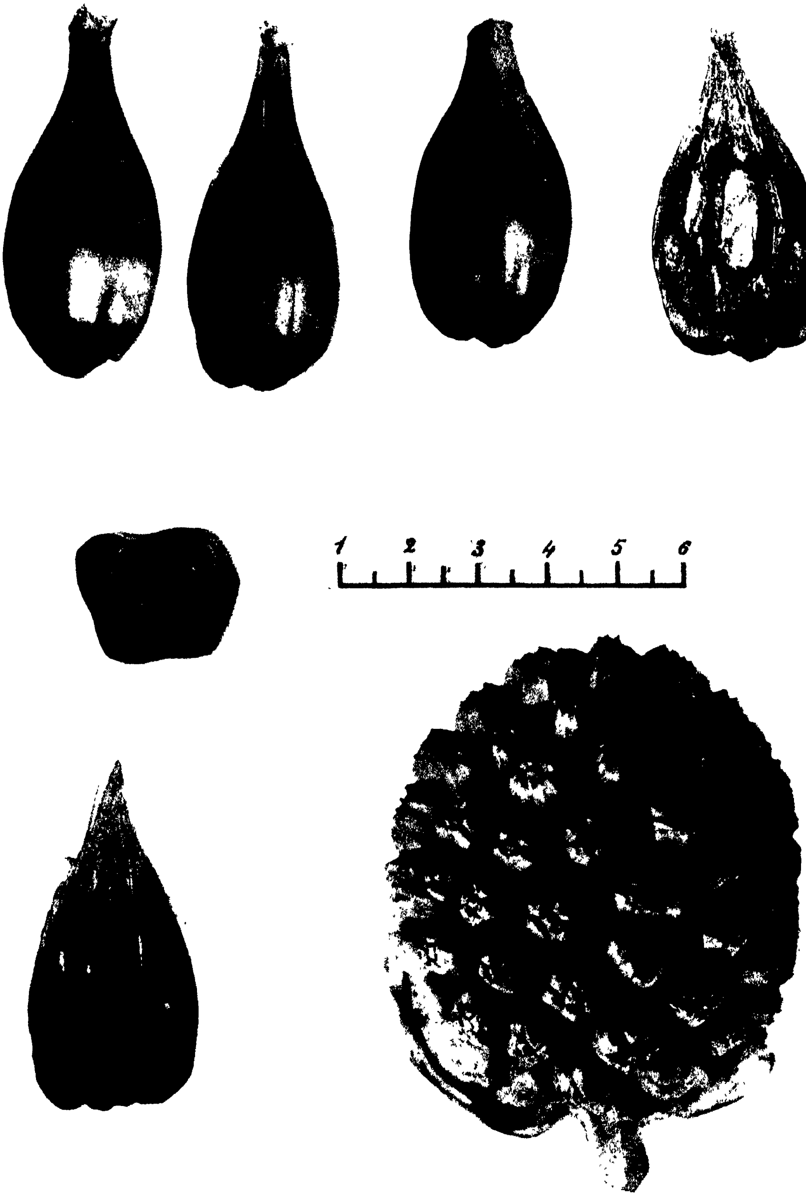
PLATE 21

Pandanus papeariensis Martelli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PANDANACEAE OF RAROTONGA

BY

UGLINO MARTELLI

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PANDANACEAE OF RAROTONGA

BY

UGLINO MARTELLI

Cook's group of islands in the south Pacific Ocean, named also "Hervey" in honor of Captain Hervey, Lord of the Admiralty, was discovered by James Cook in September 1773. It is a group of eight small islands, the chief of which is Rarotonga, about thirty miles in circumference and volcanic. Mount Tervanga, or Te-Manga, called also Taitukura or Tairukura, whose height has been calculated as 685–880 meters, is the highest on the island.

Rarotonga was not discovered by Cook, nor by the missionary, John Williams, in 1823, as is generally believed, but by a "sad" man, well known as a half-pirate, Captain Goodenough, in 1821. He kept secret his discovery of the island on account of his evil actions, having taken by deceit and kept on board some girls of Rarotonga. In October 1823, the missionary, Williams, visited Aitutaki, an island of the group north of Rarotonga, then unknown, and distant from it about one hundred fifty miles. The missionary was informed there about the rapine which had happened two years earlier. His informant was a young girl named Tapairu, cousin of a principal chief of Rarotonga, one of the ravished girls landed in Aitutaki by Captain Goodenough. In this manner the missionary came to know of the existence of the island of Rarotonga, and as the girl wished to return to her native country, he tried to discover the unknown island and after some searching, in 1823, he succeeded in landing at Rarotonga.[1]

Freycinetia Wilderi Martelli, sp. nov.

Freycinetia sp., Cheeseman, Flora Rarotonga *in* Trans. Linn. Soc. London, 1903, p. 300.

Plate 22

Repens. Folia circiter 60 cm. longa, coriacea linearia, sensim attenuato- acuminato- longiuscule-subulata, 1.5 cm. lata, fere in dimidia superiore parte subexplanata, in inferiore plicato canaliculata, in basilari, breviter sensim dilata (etiam 2.5 cm.) et amplectentia ibique ambitu convexo; lamina utriusque longitudinaliter minute crebreque manifeste rimosa, marginibus inermibus vel interdum, sed raro, in parte basilari, subito supra auriculos perpaucis (1, 2) denticulis minutissimis, remotis, notatis, in extrema parte apicali subulata, acute denticulato-serrata; costa media in pagina inferiori minima et subinconspicua, in parte apicali tantum a marginibus similiter acute denticulata; auriculis paullo manfestis, membranaceis, 5 cm. longis, angustis (ad basim circiter 5 mm. latis), sensim attenuatis acuminatis, apice adnatis. Inflorescentia ♀ terna a spathis remotiusculis convoluta; spathae basinversus naviculares et sensim dilatatae, apicem versus foliaceae, inferiores longe-attenuato-acuminato-subulatae, superiores breviores et acuminatae. Pedunculus circiter 1 cm. crassus, brevis; pedicellis subaequalibus, 30–35 mm. longis, 3–4 mm. crassis, levibus longitudinaliter striatulis (in sicco). Syncarpia immatura 6–6.5 cm. longa, circiter 1 cm. diam. cylindracea. Baccas immaturas tantum vidi, longitudinaliter compressas et dispositas, parte stigmatifera 1.5–2.5 mm. longa, 1–1.5 mm. crassa, stigmata in baccis inferioribus 7, interdum 8 vel 9, apicalibus 4–5. Semina.....

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[1] For more particulars see Thomas Cheeseman, The Flora of Rarotonga, Trans. Linn. Soc. London, 1903 (Botany), p. 261.

Habitat.—Rarotonga, Cook's group. Plentiful on mountains; *legit* Gerrit P. Wilder, no. 11 (Plantae Rarotonga), July 1929 (type in Herb. Univ. Calif. and in Herb. B. P. Bishop Mus.).

Thomas Cheeseman in his Flora of Rarotonga *in* Trans. Linn. Soc. London, 1903, p. 300, indicates a *Freycinetia* sp. very abundant on the mountains, but he could not find any flower or fruit of it. Gerrit P. Wilder, in 1929, took an interest in these plants and during four months he tried to find some of them with flower or fruit, but he did not succeed in finding more than one specimen, and it in fruit only. He sent this specimen to the herbarium of the University of California and the same was transmitted to me for identification by the kindness of Professor Setchell, to whom I am very grateful. I here describe it, as it is an unknown species, under the name of *Freycinetia Wilderi*, from the first collector of the fructified plant. Mr. Wilder informs me that the reason it is so difficult to find these plants in bloom or in fruit is because rats, very numerous on the mountains of Rarotonga, eat all the inflorescences of *Freycinetia* as soon as they begin to develop. This explains why Mr. Cheeseman did not find any and why Mr. Wilder found only one plant in fruit. The same thing was ascertained by the missionary, Delmas, to happen in the Marquesas group. We may observe, then, that before the introduction of rats into those islands by man, after their discovery, the Freycinetias must certainly have reproduced themselves by seeds as well as agamically, while now their multiplication is almost exclusively left to the agamic action, which limits the power of diffusion of these plants.

Pandanus crustatus sp. nov.

Plate 23

Arboreus. Syncarpium solitarium, oblongum circiter 12 cm. diam. (fide Wilder); phalanges numerosae, 5–5.5 cm. longae, 3–6 cm. crassae, obpyramidatae, basi angustae, acute-penta-hexagonae, fere ad tertiam superiorem partem liberae, ibique convexae, faciebus subaequalibus, latis, planis vel vix concavis, vertice phalangium rotundato, in sicco, a tegumento crusta simile, brunneo, bullato cum plurimis lenticulis sparsis linearibus, elongatis, prominulis obtecto; loculis 4, sulcis interlocularibus, causa crustae, inconspicuis. Endocarpium osseum, in parte media phalangis, 2 cm. spissum situm; in sectione longitudinali, superne dentato-rimosum, inferne leviter rotundatum. Mesocarpium superum 14–16 cm. spissum, cavernis fibroso-squamulosis; inferum 2 cm. spissum, fibrosum et medullosum.

Habitat.—Rarotonga, Cook's Archipelago. Trees scattered at about 450 m. elevation. August 1929; *legit* Gerrit P. Wilder, no. 10.

Pandanus crustatus forma minor Mart.

Syncarpium globosum, 10 cm. diam.; phalanges minores 4 cm. longae, 3.5 cm. latae. Endocarpium 19–23 mm. spissum.

Habitat.—Rarotonga, near the seashore; August 5, 1929; *legit* Gerrit P. Wilder, no. 9. Almost all the trees being rendered sterile and even killed by an introduced aphis.—Summit of Maungatea,[2] 1650 ft. (about 480 m.); *legit* Parks, C, no number.

I consider it best to regard these plants with smaller syncarps and phalanges as a form. Mr. Wilder informs us that these trees are rendered sterile and even are killed by an introduced aphis (he says nothing about whence it came or to what species it belongs). We may suppose that the *forma minor* may be a consequence of a less development, due to the pathological conditions of the plant caused by the aphis, but I would exclude that doubt because the same "*forma minor*" was collected by Mr. Wilder on the seashore where plants are killed or almost rendered sterile, and also Mr. Parks collected the same form on top of Mount Maungetea and he does not mention any damage produced there by the aphis. It therefore seems to me evident that the smaller form is natural and not a consequence of a pathological state. I consider this species and the form to be endemic, or at least introduced in Rarotonga a long time since, for the reason that it is living scattered here and there

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[2] Mount Maungatea is situated in the northern part of the island (see the map in Cheeseman, l. c.).

from the seashore up into the mountains even to a height of 450 m. The species is distinguished by having the tops of the phalanges covered by a corky, irregular crust.

Pandanus Ala-Kai sp. nov.

Plate 24

Phalanges cuneato-turbinatae, 4–5 cm. longae, sensim in basim angustissimam attenuatae, acute angulosae, lateribus inaequalibus, subplanis, fere in tertia superiore parte liberae, ibique 2.5–3.5 cm. diam., convexo-subrotundatae, loculis 3–4 vel 5, persaepe subaequalibus, rotundatis, subangulosis, plus-minusve vel parum elevatis et a sulcis itidem plus minus vel nonnihil profundis et latis separatis; stigmata prominula, latiuscula. Endocarpium, in sectione longitudinali, fere dimidia parte inferiori phalangis occupans, 25–27 mm., spissum, quasi in dimidia superiori parte acute-pyramidatum; mesocarpium superum cum cavernis latis, medulloso-fibrosis; inferum subnullum vel brevissimum, compactum.

Habitat.—Rarotonga, Cook's Archipelago, along the shore road. Harold E. and Susan Thew Parks, nos. 22650(*B*) and 22650(*A*).

This species has some resemblance, in the shape of phalanges, to those of *Pandanus upoluensis* and I think it may be an introduced species at Rarotonga. There are in the collection two specimens from the same locality and I have described that noted (*B*) because its phalanges are more normally developed than those of (*A*). I do not consider as of any phytographical importance the lenticels, sometimes very numerous, that may be observed at the top of the phalanges and at the bottom of the furrows that divide the locules.

The native name "Ala-Kai" means "edible Pandanus," but indeed the phalanges seem to be scantily provided with edible substance. Perhaps the natives eat them when they are very young and tender or, better, they eat perhaps other parts of the plants, as the bud or the roots? There is no information about this on the label.

Pandanus tessellatus Martelli

Plate 25

Arbor parva, ramoso-expansa. Syncarpia pendula tres in racemo congesto disposita, dua multo minora, inaequalia, 5 vel 3 cm. diam., globosa ad basim syncarpi majoris imposita, major oblongum 11–12 x 10–11 cm. Phalanges numerosae, parviusculae, 4 cm. longae, subpyramidatae, sensim in basim acutam protractae, penta-hexagonae subregulares acute-angulosae, lateribus inaequalibus subplanis vel vix canaliculatis, phalanges in tertia superiore parte circiter liberae, ibique convexo-subrotundatae, supra planotruncatae; loculis numerosis persaepe 8–9, interdum 6–7, parvis subaequalibus, pyramidatis, angulosis prominentibus, a sul-

cis angustis perspicuis divisis; stigma apicale robusto, elevato, superficie papillosa lata, subverticale, parte dorsali lata et in disco subrectangulare oblique protracta. Endocarpium osseum 2 cm. spissum fere subaequaliter opposite bipyramidatum, inferior basi latiuscula truncata. Mesocarpium superum circiter 1 cm. spissum; cavernis fibroso-squamulosis; infernum 1 cm. spissum, fibrosum.

Habitat.—Rarotonga, Cook's Archipelago, at Avarua, August 1, 1929; *legit* Gerrit P. Wilder, no. 13 (in Herb. Univ. Calif.).

Notes.—I am also describing this *Pandanus* from a specimen collected at Tahiti, having a solitary syncarp. This one from Rarotonga has its syncarps disposed in a compact raceme, which ordinarily should be a sufficient character for distinguishing specifically the plant of Tahiti from that of Rarotonga. But since the phalanges of these plants, both from Tahiti and from Rarotonga, are so very much alike and the two secondary syncarps are so small, I suppose that the raceme is not constant but casual, caused perhaps by cultivation, and I am of opinion that they belong to a single species. (See also Univ. Calif. Publ. Bot., vol. 17, pl. 16, figs. 3–7.)

Pisa (Italy). From the Botanical Gardens of the University. June, 1932.

EXPLANATION OF PLATES

PLATE 22

Freycinetia Wilderi Martelli

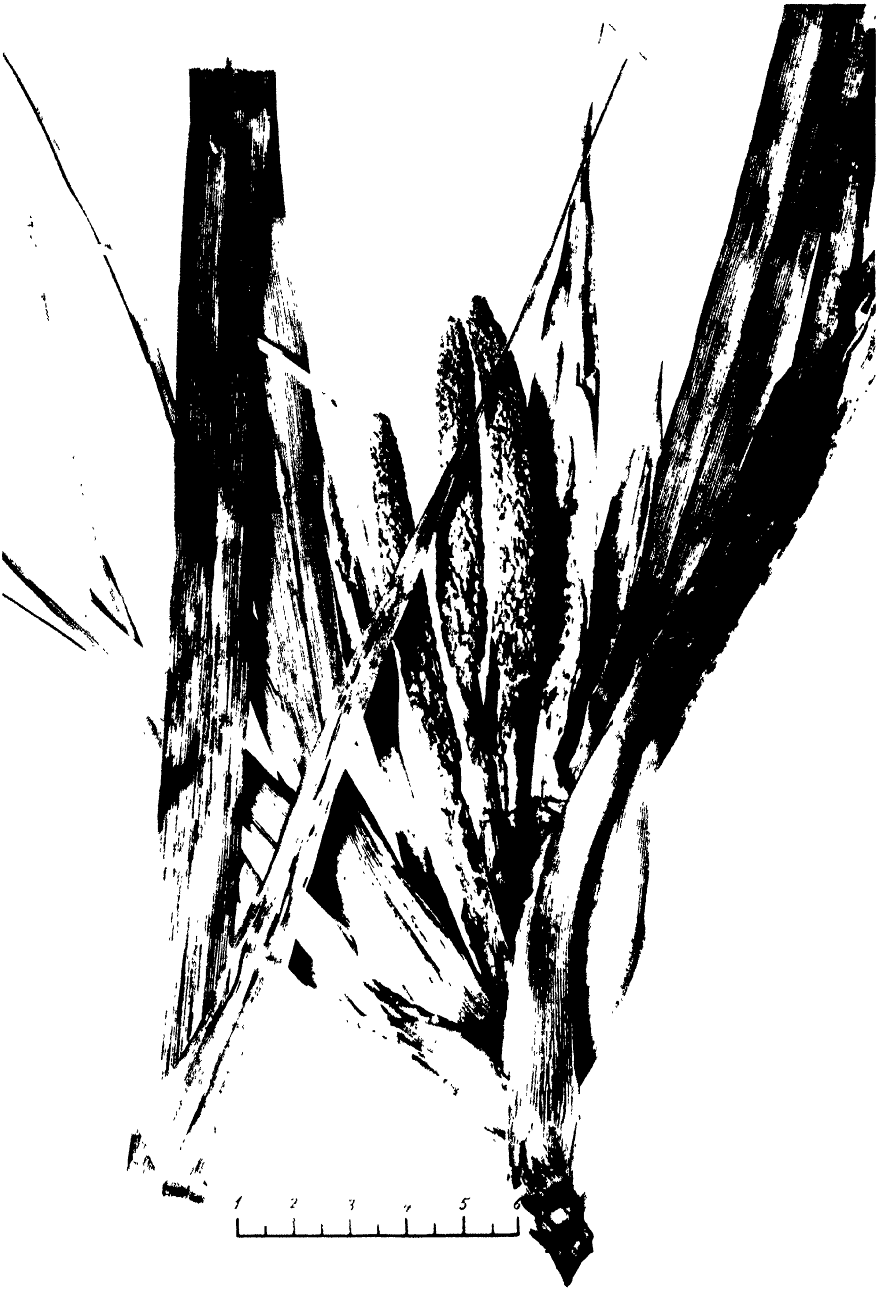
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PLATE 23

Pandanus cristatus Martelli

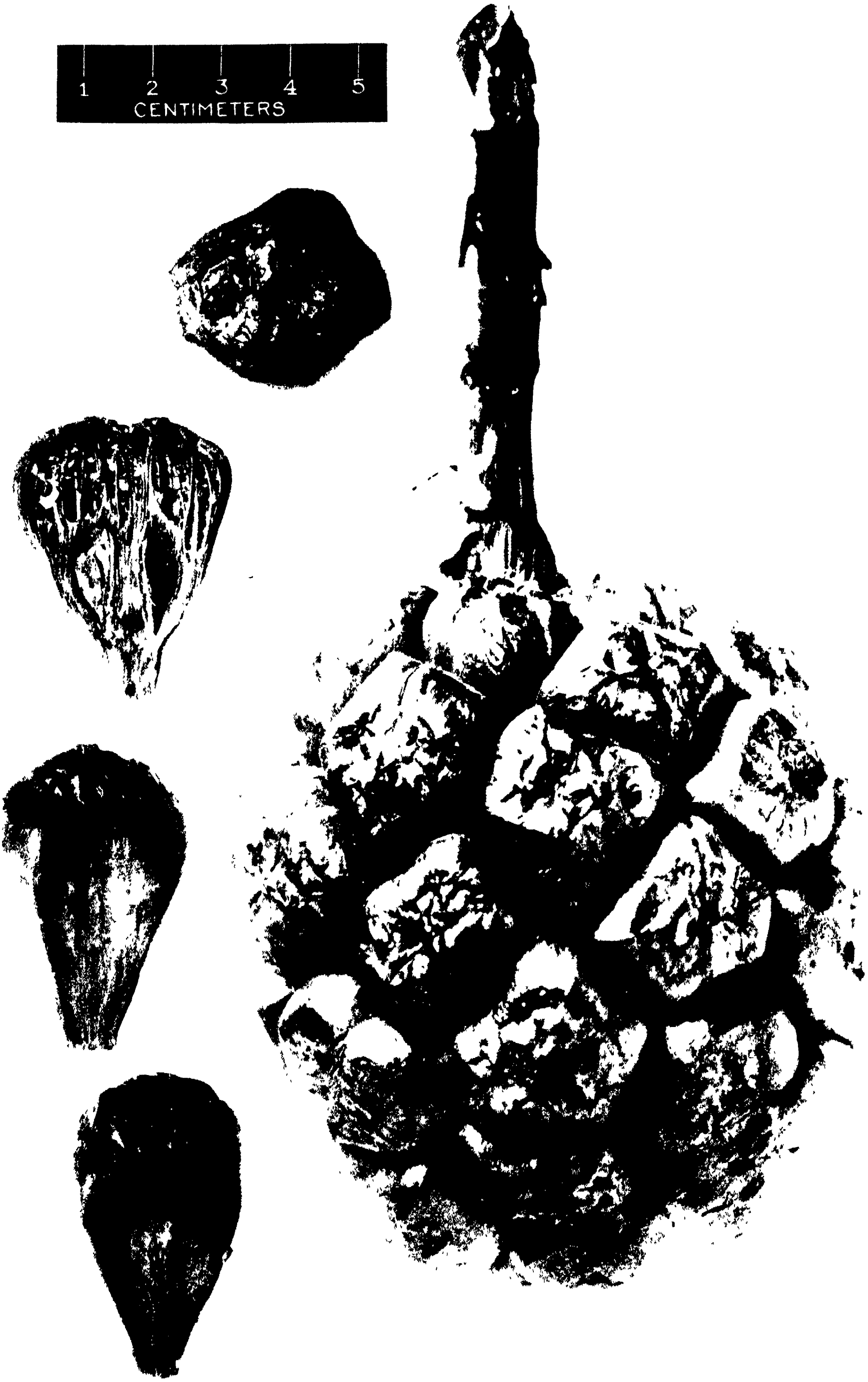
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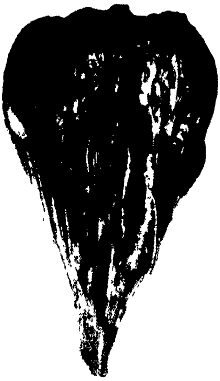
PLATE 24

Pandanus Ala-Kai Martelli



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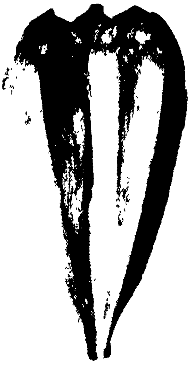

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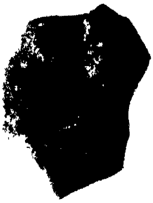

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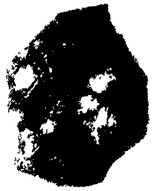

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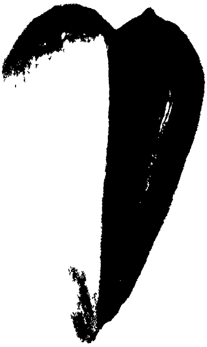

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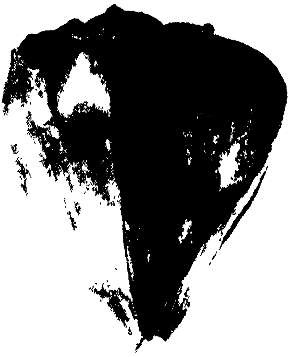

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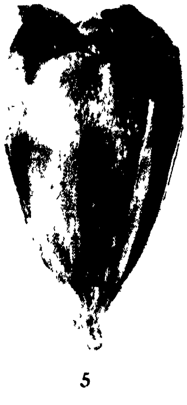

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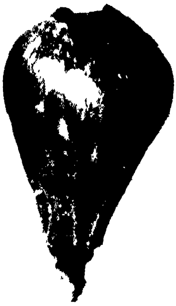

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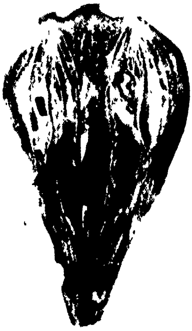

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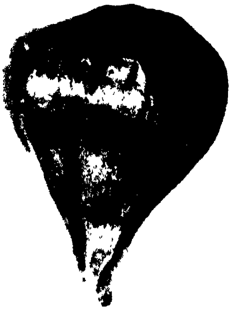

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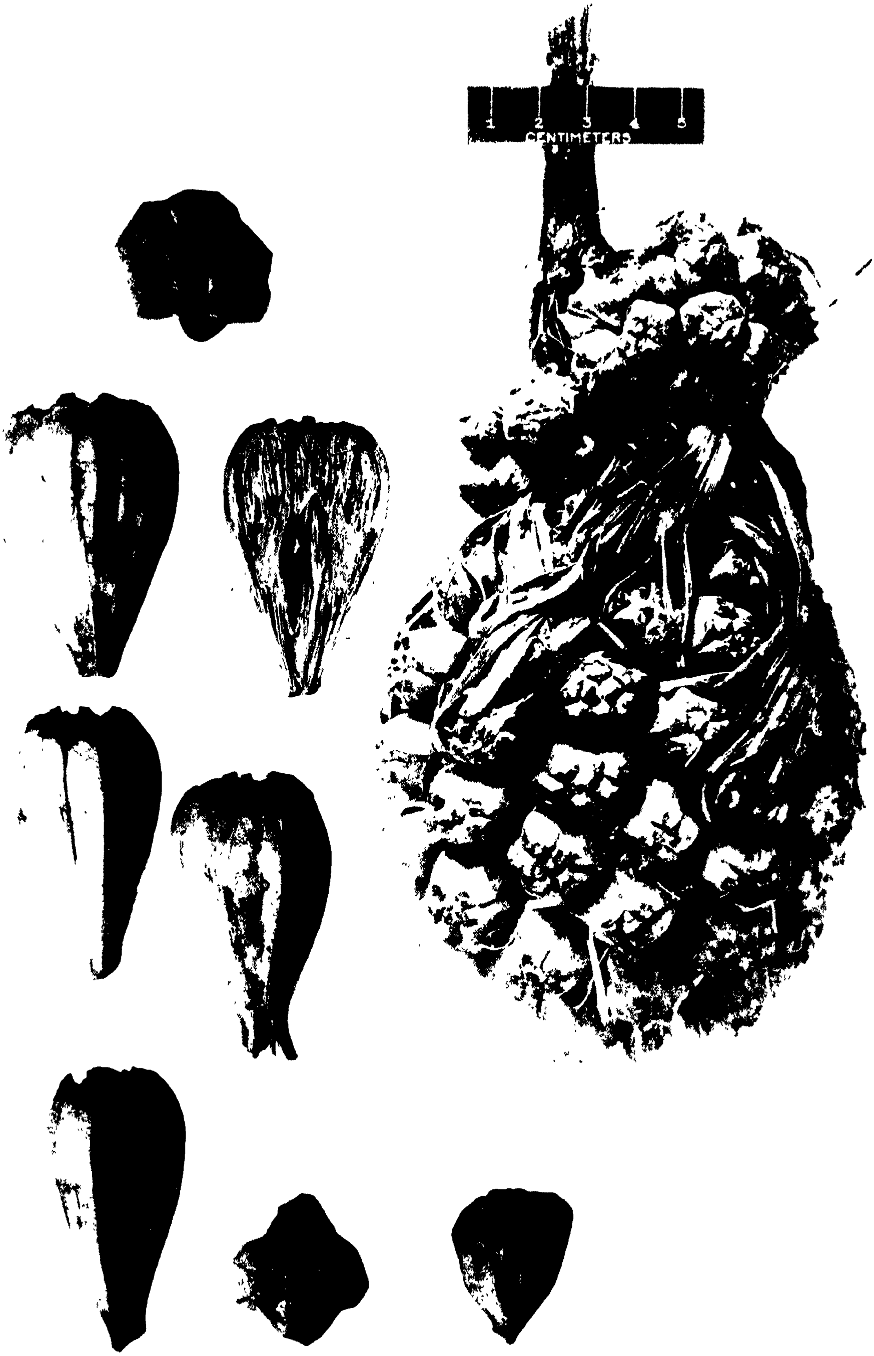
PLATE 25

Pandanus tessellatus Martelli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CENTIMETERS

SOME EARLY ALGAL CONFUSIONS. II.

BY

WILLIAM ALBERT SETCHELL

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Unraveling synonymy and determining the proper specific name, while interesting historically and after the fashion of a solution of a puzzle, delays progress of the study of the comparative morphology of a group of related plants, but must be considered essential to both monographic and distributional work. In the first instalment of these notes on Early Algal Confusions (Univ. Calif. Publ. Bot., 16 :351, 1931), introductory remarks served to explain and give reasons for the subsequent treatment of certain species whose history leads back among the earlier writers and the older herbaria containing Algae. In this contribution, certain other species, coming under investigation, will be accorded similar treatment in the hope that some of the uncertainties as to just what plants are referred to under some particular binomial may be removed and what evidence may be brought forward for the conclusions advanced.

In the last paragraphs of the first article on this subject, remarks were made as to the status of *Codium decorticatum* (Woodward) M. A. Howe and certain suggestions were put forward. Soon after printing, the possibility of a solution of the problem presented itself and was acted upon. The statement of Woodward (Trans. Linn. Soc., 3 :55, 1797), that the specimen was received from Mr. Lilly Wigg, suggested that, since Mr. Wigg had been closely associated with Dawson Turner, the type specimen might be found among Turner's specimens in Herb. Hooker. The director of the Royal Botanic Gardens at Kew replied to an inquiry that such a specimen was thus represented and most graciously permitted it to be studied. *C. decorticatum* (Woodw.) M. A. Howe has already been discussed in the preliminary paper (see Univ. Calif. Publ. Bot., 16 :360, 361, 1931). The type specimen at Herb. Kew is fully equal, in respect of length, to the dimension given in the type description (pl. 26, fig. 1). The illustration shows well its habit and stature, a size equaled only by that of *C. Chazaliei* W.-v. Bosse and the eastern Asian *C. cylindricum* Holmes. As to these, the identity of the former is not yet settled, but it seems likely that the two may be of the same species, both having huge utricles (see plate 29, fig. 1) and neither species having been described as showing any decided flattening below the dichotomies.

In the latter, the flattening below the dichotomies varies, but seems usually to be present at some of the dichotomies and, at least in large plants, often remarkably dilated, while in other dichotomies of such a plant there may be no trace even of compression. Other species which differ somewhat in habit from *C. decorticatum* (as limited to type) are *C. longiramosum* S. and G. (Proc. Calif. Acad. Sci., ser. 4, 12 :710, pl. 15, fig. 27, and pl. 37, 1924) and *C. amplivesiculatum* S. and G. (*loc. cit.*: 709, pl. 15, figs. 28, 29, and pl. 35). At present, it seems best to consider *C. decorticatum* (Woodw.) M. A. Howe as distinct from these eastern Pacific species as well as from the other species of the Pacific coast of North America placed provisionally under *C. decorticatum* by Setchell and Gardner (Univ. Calif. Publ. Bot., 8 :173, 1920 and Proc. Calif. Acad. Sci., ser. 4, 19 :130, 1930). It also seems, and most definitely, to differ in both habit and utricle characters from the types, at least, of *C. elongatum* Ag., *C. lineare* Ag., and *C. decumbens* Martius, as indicated farther on.

Codium elongatum C. A. Agardh was described in 1820 in the first part of the Species Algarum (p. 454). The species was evidently founded upon a specimen from Cadiz in Spain, and its specific character indicated by diagnosing it as "*fronde dichotoma compressa ad axillas dilatata.*" Compared with a photograph of the type specimen (see pl. 26, fig. 2) obtained through the kindness of Professor Harald Kylin, Agardh's plant was a low species and very similar in habit to those illustrated by Montagne in the Flore d'Algérie (Atlas, pl. 13, fig. 1, *a*, *b*, *f*, 1850) and by Kuetzing in his Tabulae Phycologicae (vol. 6, pl. 96, 1856).

Agardh, however, quotes two synonyms. His first is *Ulva decorticata* Woodw., although it seems certain that he had never seen the type specimen, and in his description he quotes from that of Woodward as to length, ". . . . 2 cubitalis," but he also notes that Woodward describes his species as "*cylindrica.*" His second synonym for *Codium elongatum* is "*Agardhia areolata* Cabrera in Phys. Sälsk. Årsber.," a reference which has been puzzling to most if not all students of Algae. It is to be noticed, no volume or page is quoted for these references for the *Agardhia* of Cabrera or for any of the species which must have been made known previous to 1820 (earliest date given for the first volume of C. A. Agardh's Species Algarum). Search has revealed only a brief statement in Physiographiska Sällskapets Årsberättelse aflemnad as dese sekreterare den 6 Maj 1823, published at Lund in 1823. On page 29 is a short article entitled, Descriptio novi generis Algarum, auctore Antonio

Cabrera, Canonico Gaditano. There follows a statement (in Swedish) that this genus, called by the author *Agardhia,* is the same as that called *Codium* in Agardh's Species Algarum. A list of 6 species follows, the equivalents in Agardh's Species Algarum being given in each case. Whether this is the only publication of the *Agardhia* of Cabrera and of his species is not yet perfectly established. Thus far, no further reference has been found in the progress of this investigation.

A utricle of the type of *Codium elongatum* Ag. is represented on plate 29, figure 2, for comparison with one of the type of *C. decorticatum* (Woodw.) M. A. Howe. In both habit and details of the utricle structure, the two types are sufficiently distinct to be kept separate. The medium size of the utricles and the tendency to flatten, but not to become completely flat, together with these habital differences and the attendant tendency to infra-axillary dilation, distinguish the species. No. 471 of the Phykotheka Universalis, collected at Oporto, Portugal, therefore not far from the type locality, seems typically *C. elongatum* Ag., at least with reference to the type specimen.

Codium lineare was described by C. A. Agardh, in 1820, on page 455 of the Species Algarum. It was also collected at Cadiz by Cabrera, who mentions it (in 1823) as *Agardhia ramentacea* Cab. It is described thus: "*fronde plana furcata lineari tuberculata.*" It is said by Agardh to differ from *Codium tomentosum* and *C. elongatum* in being a shorter and less branched plant, not dilated at the axils, and in being more rigid and tuberculate. The habit of the type specimen is shown in the photograph, kindly provided by Professor Harald Kylin, reproduced on plate 27, figure 1. J. G. Agardh (Lunds Univ. Årsskr., 23:45, 1887) places the species, which he confesses is little known to him, with his "*Elongati,*" as being "ni fallor complanata." The photograph of the type specimen tends to support this conditional statement. The question as to its relationship has been variously answered, or suggested. It has been considered as an independent species by many, but, without reference to the type specimen, some have referred it to *C. elongatum* Ag., while J. G. Agardh (Lunds Univ. Årsskr., 23:45, 1887) includes under *Codium lineare* Ag. the *C. decumbens* Martius of Brazil.

From a consideration of the type it may be doubted whether the frond is really complanate; rather it is deformed by the numerous short proliferations which are, in turn, seldom dichotomous (or proliferate). It seems likely to be of the general style of the proliferous or deformed specimens of *Codium dichotomum* (Huds.) Setchell (*C. tomentosum* Auctt.), of *C. vermilara* (Bertol.) d. Chiaje, or of *C. elongatum* Ag., mentioned in the literature or distributed in various *Algae Exsiccatae* or by various phycologists. Such are *C. tomentosum* var. *proliferum* Kuetzing (in Hohenacker's Meeralgen, No. 497) and Adriatic specimens named *C. tomentosum β digitatum* or *C. elongatum* var. *monstruosum* Mont.

The utricles (see pl. 29, fig. 3) of the type specimen average much smaller than those of the type of *Codium elongatum* Ag. and at the same time differ somewhat in shape and thickening of apical membrane from typical utricles of the Atlantic *C. dichotomum*. They much more closely resemble those of the Mediterranean *C. vermilara,* which may prove to be distinct, at least varietally, from typical Atlantic *C. dichotomum*. From *C. decumbens* Martius, as represented by cotypes, the utricle is much smaller and the habit seems different, as will appear from what is written below.

Codium decumbens Martius has been placed under *C. lineare* Ag. ever since J. G. Agardh, as indicated above, placed it there in his revision of the genus *Codium*. O. C. Schmidt, in his monograph (Bibl. Bot., Heft 91, p. 58, 1923) seems to have drawn up his description of *C. lineare* and made his drawings of utricles from cotypes of Martius, preserved in Herb. Munich and Herb. Hamburg. Professor Dr. W. Robyns of the Jardin Botanique de l'État at Brussels has been so kind as to have thorough search made for the type in Herb. Martius, but has not been able to locate it. Cotypes are in Herb. Hamburg and Herb. Munich and through the generous cooperation of Professor Dr. E. Irmscher of the former and of Professor Dr. Carl von Schoenau of the latter it has been possible to examine them. The cotypes are not well prepared specimens, as Schmidt (*loc. cit.*) has already indicated. They seem to belong to a low species (see pl. 27, fig. 2), apparently complanate throughout, and without indication of a decumbent habit. There is in Herb. Martius, at Brussels, a specimen labeled *Codium decumbens,* no. 2445, A. Glaziou, collected in "Prov. Rio de Janeiro, 1868," which seems to be correctly named (see pl. 27, fig. 3), and in Herb. University of California two specimens, nos. 341344, 341345, collected at Puerta de la Palma, Uruguay, by Carmen de Franc, which (see pl. 28) seem also to belong to the same series of forms. While these specimens resemble somewhat in habit the *Codium elongatum* Ag., the better developed plants show clearly a greater flattening throughout the frond and the utricles of both cotypes, and the other specimens are much larger than those of the type specimen of *C. elongatum* Ag. The utricles (see pl. 30) are, in fact, very large, much of the same sizes, but of shapes slightly differing from those of *C. decorticatum* (Woodw.) M. A. Howe. In a recent paper on certain algae from Uruguay (Bull. Torrey Bot. Club, 57:606, 1931), M. A. Howe has placed *C. decumbens* Martius under *C. decorticatum,* but with a query. Since, as indicated earlier, the type specimen of *Ulva decorticata* Woodw. is almost if not strictly cylindrical, it seems fairly certain that *C. decumbens* Martius is to be regarded as an autonomous species and one which probably extends along the tropical Atlantic coasts of the Americas from Uruguay in the south to the Caribbean coasts in the north.

While I was attempting to work over various species of *Sargassum* from the Hong Kong (see Setchell, Hong Kong Naturalist, Suppl. **2**: 33–49, pls. 4–20, March, 1933) and central Pacific areas, the confusion attending the earlier and more modern names and descriptions became so apparent that attempts to stabilize the nomenclature and specific concepts seemed urgent. One group of entities centers about the group passing under the names of *Sargassum serratifolium* (Ag.) Ag. and *S. tortile* (Ag.) Ag. The various forms to be placed under these names range from the Strait of Tsugaru, between the islands of Honsho and Hokkaido, Japan, down to Hong Kong and Macao. One *Sargassum* is quoted from Kamtschatka, but undoubtedly it grew much farther south.

The oldest names suspected to belong to members of this group were given by Dawson Turner in his Fuci, and Turner may almost be said to have given the first intelligible account of the species of the section of the old genus *Fucus* which we now segregate as *Sargassum.* Turner described or distinguished anew about 36 species of *Sargassum,* of which 11 were based wholly or partly on specimens from the eastern coast of Asia. Turner's specimens were mostly from Professor F. K. Mertens of Bremen and many of his, in turn, were collected by Dr. Horner. Some of these specimens were retained by Turner and are to be found in Herb. Hooker at Kew. A few, however, are not to be found and may have been returned to Mertens, the sad loss of whose collection of exotic algae is related by himself (Mem. Mus. d'Hist. Nat., Paris, 5:173–174, 1819). It may be that the missing types were among them. Some of the type specimens are fragmentary, battered, bleached, or otherwise far from satisfactory, but the plates of the Fuci, in general, show fairly the nature of the plant Turner had before him. Turner's work was regarded with especial reverence by both C. A. and J. G. Agardh (Univ. Calif. Publ. Bot., 16:354, 1931) and there is little evidence in the literature that Turner's type specimens have ever been restudied; at least this seems true for the *Sargassa.*

Through the extreme courtesy of the director of the Royal Botanic Gardens at Kew, Sir Arthur W. Hill, search was instituted for all Turner's types and as many as could be found were made accessible for study. In this way it was possible to go over Turner's eastern Asiatic types so far as they could be located. Unfortunately, only two of the four type specimens having to do with the *serratifolium-tortile* group could be located in Herb. Kew, so that Turner's descriptions and figures must guide in determining priority of name and nature of certain of the plants designated. When, however, a considerable number of specimens from the same locality and from neighboring localities is available, and is collected at various seasons, there is opportunity for observing variation and for considering various states, which assists materially in dealing with figures and descriptions as conscientiously prepared and drawn up as were those of Turner. It seems therefore not at all rash to review the attitude of various writers on this group of species and to advance certain opinions as to the proper status of each important reference in the literature. The work of the Japanese botanists Yendo and Okamura has assisted materially in the attempt to unravel the complexity now existing.

The group of species, varieties, forms, and states to be discussed belongs to J. G. Agardh's subgenus *Bactrophycus,* having in common compressed or angulate main laterals and middle fulcrant (or supporting) costate phyllodes (vertical leaf-like laterals of determinate growth) with margins distinctly to deeply serrate. The lowest phyllodes may be entire or dentate and the uppermost phyllodes (on the inflorescences) of luxuriant plants may be elongated, very narrow and entire. The lowest phyllodes and the branches or branchlets from the main laterals are retroflex, and the phyllodes themselves are twisted into a horizontal position. The receptacles are either antheridial or oogonial, simple, longer or shorter, broader or narrower, siliquaeform, and usually arranged in a simple raceme.

Turner described the first species belonging to the group, but his descriptions and plates are all there is to indicate the nature of his plants, which were non-characteristic scraps. They may fairly satisfactorily be matched from similar fragments among the larger collections examined from Hong Kong, contributed through the energy and kindness of Dr. G. A. C. Herklots.

Fucus Siliquastrum Mertens (see Turner, Fuci, 2:26, pl. 82, 1809) was the first member of the group to be described. The specimen was sent to Turner by Mertens with the name under which it was published.

It was collected at Nagasaki, Japan, by Dr. Horner. No type specimen can be located in Herb. Hooker at Kew. The type materials evidently consisted of broken pieces of one frond with the "stem" (of undetermined length) three-sided and angulate. The broken portions have branches, spirally placed, a foot to a foot and a half long. The characteristic fulcrant phyllodes are represented by scars, but the extreme bracts are long, narrowly linear, and show no evidence of dentation, but are provided with an extremely narrow dark midrib. The bladders are slightly obovoid, with a short mucro at their apices. The receptacles are evidently oogonial and siliquaeform, characteristic in general of the *Bactrophycus* species of *Sargassum*. The description and figures of Turner may readily be matched by fragments from Shau-ki-wan and from Repulse Bay, Hong Kong, and by the upper parts of plants having below the characteristic fulcrant leaves of *Sargassum serratifolium* (Ag.) Ag. or of *S. tortile* (Ag.) Ag. Plate 31 shows a scrap very similar to that used by Turner for his description of *Fucus Siliquastrum* Mertens, which became *Sargassum Siliquastrum* (Mert.) Ag. The angulate stem, the elongate slender costate bracts, the obovate mucro-tipped vesicles, are its characteristics.

The second species described is *Fucus scoparius* Turner (Fuci, 2:156, pl. 132, 1809) or *Sargassum scoparium* Ag. The specimen was collected in the Strait of Corea by Dr. Horner, and was also sent to Turner by Mertens. No type specimen can be located in Herb. Hooker at Kew, but Hong Kong plants (see pl. 32) closely resemble Turner's figure. The resemblance to *Fucus Siliquastrum* Mertens is close, although the plant seems to be antheridial. Turner notes the close resemblance to *F. Siliquastrum* but states that *F. scoparius* is "immediately distinguishable from it by the very remarkable circumstance of its producing upon the same shoot both simple and pinnatifid leaves." These "pinnatifid leaves" certainly seem to be the upper very narrow alternately toothed fulcrant phyllodes of the *S. serratifolium-tortile* group. The receptacles are the narrower, less flattened, siliquaeform structures characteristic of antheridial plants. The type of *Fucus scoparius* Turner represents a stage between *F. Siliquastrum* Mertens and readily recognizable plants of the *serratifolium-tortile* group. Turner evidently had two specimens of this group which showed more typical leaves than did his specimens of *Fucus Siliquastrum* and *F. scoparius*. He referred these as varieties under his *Fucus longifolius* as var. *tenuifolius* and var. *angustifolius* (see Turner, Fuci, 2:88, pl. 104, figs. *b, c, d,* 1809). The reference of these varieties to *F. longifolius* seems somewhat strained. The type of *F.*

longifolius itself is, according to Turner, in the Linnean Herbarium, where it existed without remark or locality. Esper (Ic. Fucorum, 2:57, pl. 25, 1798) had evidently described and figured a plant of the same species (under the much abused name of *Fucus salicifolius*) which he feels fairly certain came from the East Indies but in which he was apparently mistaken. Later, it was referred to *Sargassum* by C. A. Agardh (Spec. Alg., 17, 1820) but without any additional data. J. G. Agardh (Spec. Alg. I:283, 1848) referred under it certain plants from the Cape of Good Hope region (where it evidently belongs), but later (Spec. Sarg. Austr., 128, 1889) rejects it as being a *Sargassum* and suggests that it may be a *Carpophyllum*. Kuetzing (Spec. Alg., 605, 1849 and Tab. Phyc., 10:23, pl. 64, 1860) places it under his genus *Anthophycus*, while Grunow (Verh. k. k. zool.-bot. Gesell., Wien, 65:363, 364, 1918) designates it as of all the Sargassums the most beautiful and disturbed by no doubts. The typical *Sargassum longifolium* (Turn.) Ag. has been brought forward in such detail, because it has been quoted as a synonym of species of this group with which the specific type has very little if anything in common.

It is different, however, with the two varieties of *Fucus longifolius* described by Turner. C. A. Agardh (Alg. Decas Quart., 41, 1815) quotes *Fucus longifolius* var. *tenuifolius* of Turner under his newly described *F. serratifolius* and the *Fucus longifolius* var. *angustifolius* Turner under his *F. tortilis* (C. A. Agardh, *loc. cit.*, p. 42), where they have remained unchallenged until the present day. Types of these varieties of Turner are to be found, and Turner's figures *b, c,* and *d* of his plate 104, representing his variety *angustifolius,* seem distinctive of what is usually known as *Sargassum tortile* (Ag.) Ag., and his description of his var. *tenuifolius* seems to fit the Agardhian description of *S. serratifolium.* These will be more definitely characterized farther on, but the first variety is stated by Turner to have thin leaves with a texture between membranaceous and chartaceous, while the second, presumably with the leaves thicker and firmer, is said to have the leaves linear, very narrow, serrate-dentate, with the teeth reaching down to the midrib. The latter variety recalls the states of the plants described by Turner under both *Fucus Siliquastrum* and *F. scoparius.*

C. A. Agardh added to the group under discussion in his Four Decades of Algae (1812–1815). In the first Decas Algarum (1812) he described *Fucus tortilis* Ag., the type of which was sent by Tilesius, said to be from Brazil, the locality, however, being doubted by J. G. Agardh (Spec. Alg., I:292, 1848), and Kuetzing (Phyc. Gen., 367, 1843) giving only Japan. C. A. Agardh, however, restricts his *Fucus serratifolius* var. *angustifolius* to the Liu Kiu Islands of Japan, whence the specimens also were sent by Tilesius. C. A. Agardh does not quote the *Fucus longifolius* var. *angustifolius* Turner under his variety in this reference but in the Algarum Decas Quarta (p. 42, 1815) he indicates that his species *F. tortilis* includes Turner's variety. In the fourth Decade (p. 41, 1815), C. A. Agardh describes his *Fucus serratifolius* from specimens collected near Satsuma, Japan, and sent to him by Tilesius. Since these two species are even yet being kept separate and stand as models for the general group, it seems desirable to examine the characters assigned to them by C. A. Agardh. Unfortunately, the types, preserved in Herb. Agardh at Lund, are not immediately available for detailed comparison.

The type specimen of *Fucus tortilis* Ag. is evidently a long plant but seemingly without a holdfast; at least C. A. Agardh does not mention a holdfast. It is also sterile, with triquete contorted stems, and linear, deeply serrate phyllodes which are free or inserted on spherical, subteretely petiolate vesicles. The vesicles in variety *angustifolius* (*"augustifolius"* through misprint) are oblong and the phyllodes are very narrow. Thus far runs the diagnosis. The more detailed description adds little except that the texture is coriaceous; the "leaves" are 2–4 inches long and simply serrate; the stipular petioles of the "leaves" are plane and connate at the base with the axes; the vesicles have filiform petioles almost 5 lines (10 mm.?) long with the vesicles in median position (vesicles apiculate or petiole prolonged beyond the vesicle). This seems certainly to be the plant later set off by the Japanese writers, Yendo (Fucaceae of Japan, 85, pl. 12, figs. 1–8, 1907) and Okamura (Icon. Jap. Algae, 5:26, pl. 208, 1924), both of whom, after prolonged experience with the Japanese plants of this group, express the opinion that it is with difficulty to be constantly and readily distinguished from varieties or states of *Fucus serratifolius* Ag. Both writers also place as synonyms under it, *Fucus Siliquastrum* Turner, *F. scoparius* Turner, *F. longifolius* var. *angustifolius* Turner, and various species or varieties of later authors.

In Algarum Decas Quarta (1815, p. 41), C. A. Agardh describes the second species of the group under discussion, *Fucus serratifolius* Ag., from specimens sent by Tilesius, collected near Satsuma, Japan. His diagnosis calls for a plant with plane stem, divaricate alternate branches, linear duplicate-serrate "leaves," and petiolate, foliiferous, spherical vesicles. From the detailed description, we learn that the type the *Halochloae* (p. 363). In the first family, *Turbinaria, Carpophyllum,* and *Phycobotrys* were separated from *Sargassum* (as typified by *Sargassum vulgare* Ag.) and from *Pterocaulon* (as typified by *S. Peronii* (Turn.) Ag.), while in the second *Spongocarpus* (as typified by *Sargassum Horneri* (Turn.) Ag.), *Halochloa* (as typified by *S. scoparia* (Turn.) Ag. and its group), and *Carpacanthus* (as typified by *Sargassum parvifolium* (Turn.) Ag.) were segregated from C. A. Agardh's genus *Sargassum* and from one another. In this generic segregation, there is some foreshadowing of the subgenera and other divisions of *Sargassum* later proposed by J. G. Agardh (Spec. Alg., 1:274–283, and Spec. Sarg. Austr., 32–34, 1889). The *Siliquastrum*-complex is placed in *Halochloa* as *H. Siliquastrum* (Turn.) Kuetz., *H. scoparia* (Turn.) Kuetz., *H. serratifolia* (Ag.) Kuetz., and *H. tortilis* (Ag.) Kuetz., the combinations having been first proposed in the Bot. Zeit., 1843. *Sargassum macrocarpum* Ag. does not receive consideration as such, either among the *Halochloa*-species or elsewhere in the Phycologia generalis, but was considered in the Species Algarum of Kuetzing, of 1849. In 1849, Kuetzing added two species to the 1843 list and suppressed one species. The added species were *H. pallida* (Turn.) Kuetz., not a member of the *Siliquastrum*-group, and *H.* (?) *macrocarpa* (Ag.) Kuetz. Kuetzing suppressed his *H. longifolia* (Turn.) Kuetz., instituting instead *Anthophycus longifolius* (Turn.) Kuetz. to receive typical *Fucus longifolius* Turn., and placing Turner's var. *tenuifolius* under *Halochloa serratifolius* (Ag.) Kuetz. The Turner and C. A. Agardh species of the *Siliquastrum*-complex, then, are all retained in Kuetzing's *Halochloa.*

Halochloa tenuis Kuetz. (Bot. Zeit., 1843, p. 56; Phyc. Gen., 367, 1843) has been later recognized by Kuetzing (Tab. Phyc., 10:35, 1860) as not separable from his *H. Siliquastrum.* It was founded on a specimen from Japan sent out by Tilesius. The binomial may be considered as a synonym under *Sargassum Siliquastrum* (Turn.) Ag.

Halochloa macracantha Kuetz. (Bot. Zeit., 1843, 55; Phyc. Gen., 366, 1843; Spec. Alg., 633, 1849; Tab. Phyc., 10:34, pl. 97, II, 1860), a Tilesius specimen from Japan, is regarded by various writers, and for good reason, as not separable from *Sargassum tortile* (Ag.) Ag. Yendo (Fuc. Japan, 89, 1907) places *Halochloa macracantha* Kuetz. under his *Sargassum tortile* var. *macrocarpa,* which in turn seems to be only a state of *Sargassum Siliquastrum* (Turn.) Ag., as indicated earlier in this discussion.

Halochloa polyacantha Kuetz. (Bot. Zeit., 56, 1843; Phyc. Gen., 367, 1843; Spec. Alg., 633, 1849; Tab. Phyc., 10:34, pl. 98, fig. I, 1860) is regarded by Yendo (Fuc. Japan, 89, 92, 1907) as founded upon a basal portion of *Sargassum tortile* var. *macrocarpa* (Ag.) Yendo. Judging from the plate of Kuetzing, it may be more likely such a portion of *S. serratifolium* (Ag.) Ag. It seems to be only a state under the broader concept of *Sargassum Siliquastrum* (Turn.) Ag.

Halochloa micracantha Kuetz. (Bot. Zeit., 1843, 56; Spec. Alg., 633, 1849; Tab. Phyc., 10:34, pl. 98, II, 1860) and *H. miracantha* (misprint in Phyc. Gen., 367, 1843) were founded on a Tilesius specimen from Japan. The specimen is fragmentary and sterile, but Kuetzing detected that the seemingly bleached pinnules (or divisions of the leaf or phyllode) of his specimen sometimes had 2–3 narrow teeth at their apices. This seems like a character of *Sargassum serratifolium* (Ag.) Ag. and, therefore, to be reduced under the broader *Sargassum Siliquastrum* (Turn.) Ag. Yendo (Fuc. Jap., 123, pl. 15, figs. 10–17, 1907) refers to Kuetzing's species certain Japanese plants which, presenting leaves of similar shape and texture to those of *Halochloa micracantha* as represented on the plate of Kuetzing, have concave receptacles more or less minutely toothed on the apex or margins, and in some cases instead of the usual solitary position with a leaflet at the base of each, are "borne racemosely on a poorly developed minor branchlet." Together with *Sargassum nigrifolium* Yendo and *S. Kiushianum* Yendo, he has separated a group, the *Micracantheae,* to receive the three species. *Sargassum nigrifolium* Yendo, so far as habit indicates, does not belong to the same group with *S. micracanthum* (Kuetz.) Yendo and *S. Kiushianum* Yendo and, consequently, may be left out of account for the present. *Sargassum Kiushianum* Yendo, apparently founded on a single plant, is to be distinguished, according to its proposer, from *S. micracanthum,* as Yendo understands it, only by the "membranaceous character of the leaves, the extremely narrow laciniae, and the solitary receptacles." Okamura (Icon. Jap. Algae, 5:51–54, pl. 214, 1924) has described, illustrated, and discussed the two species. He does not agree with Yendo that there are two species; *S. Kiushianum* Yendo, to him, "seems merely to be a form" of *S. micracanthum,* "perhaps grown in a protected place and hence with soft membranous leaves." Okamura's opinion seems likely to be the correct one and he seems also to add to the proper elucidation of the *Micracantheae* of Yendo, when, after saying of the *S. micracanthum* of Yendo that the character of the receptacle distinguishes Yendo's selection to represent Kuetzing's species from *S. Horneri*

(Turn.) Ag., *S. filicinum* Harv., and *S. tortile* (Ag.) Ag., he goes on to say that *Sargassum micracanthum,* as understood by Yendo, resembles all three of the species mentioned in external appearance and in the shape of the leaf, but the "character of the receptacle" differs from all of them. He also mentions that *Sargassum Horneri* and *S. filicinum* differ as to the sterile forms, in the shape of the vesicle, and "*S. tortile* which is often confounded with the present species" (*S. micracanthum*) "on minute and slender habit of the frond and general appearance." It is certainly true that *S. Horneri* (Turn.) Ag. is readily distinguished from any and all of the species mentioned in having elongated vesicles (2.5 to 7 times as long as broad), but in *S. filicinum* Harv., although it is diagnosed to have spherical vesicles, these do not seem always to be exactly spherical, their shape being closely approached by the vesicles of the *S. Siliquastrum* assemblage, several of which were originally described as having spherical vesicles. *Sargassum filicinum* Harvey (Proc. Am. Acad., 4 :327, 1859) was described from a specimen with solitary, terminal, elongated, antheridial conceptacles and closely approaching *S. micracanthum* (Kuetz.) Yendo in habit and texture of leaves, as is indicated by a photograph of Harvey's type specimen received many years ago from Professor E. Percival Wright. Yendo's fragmentary specimens from Misaki, referred to *S. filicinum* (Fuc. Jap., 80, pl. 12, fig. 9, 1907) are also antheridial and seem too closely related to *S. micracanthum,* as understood both by Kuetzing and by Yendo, to be separated from it. The texture and habit of this narrower assemblage is definite but may, however, be due to the influence of a more quiet and more directly illuminated habitat. As to the receptacles, and their arrangement with occasional abbreviated, bractless racemes—they are frequently found also in the members of undoubted *Siliquastrum*-types. The oogonial receptacles of the *Siliquastrum*-types are flattened to concave, notched at the tip, but frequently with additional apical and lateral notches, at times giving an undulate to dentate outline. The dentate outline is more likely to be found in older receptacles which are discharging or have discharged their spores. The members of the *micracanthum-filicinum* complex, while representing an extreme of habit, texture, and aggregation of receptacles which are crispate or dentate on their margins, are so definitely linked, in all their various peculiarities, with the *Siliquastrum*-complex, that they may be separated only in extreme forms (see Okamura, Icon. Jap. Algae, 5: pl. 204, 1924).

Halochloa pachycarpa Kuetz. (Bot. Zeit., 1843, 55; Phyc. Gen., 366, 1843; Spec. Alg., 634, 1849; Tab. Phyc., 10:34, pl. 96, 1860) was founded on a Japanese specimen of Tilesius, communicated by Henschel. The plate shows a *Siliquastrum* antheridial plant, near to the *Sargassum macrocarpum* Ag.-type. The twisted axes and the phyllodes are of the *S. tortile* (Ag.) Ag.-type. It is not essentially different from the *Halochloa scoparia* (Turn.) Kuetz. plate of the Tabulae Phycologicae (10: pl. 95).

In 1848 J. G. Agardh, son of C. A. Agardh, issued the first volume of his Species Algarum, devoted to the Brown Algae. In this volume, which was published after Kuetzing's article in the Botanische Zeitung of 1843 (Ueber die Eigenthümlichkeit der Vegetation in den chinesischen und japanischen Meeren) and Kuetzing's Phycologica generalis, but immediately preceded Kuetzing's Species Algarum of 1849, Agardh thoroughly revises *Sargassum,* both as to subdivisions and as to species. In all, J. G. Agardh treats of 124 species of more or less certain position. The *Siliquastrum*-group is placed in his section II. *Arthrophycus* (with retroflex branches or branchlets and phyllodes becoming horizontal by torsion) and in Tribe III, *Holophylla* (with angulate stem, non-pinnatifid phyllodes, and simple axillary receptacles). The five species of C. A. Agardh, *Sargassum siliquastrum* (Turn.) Ag., *S. scoparium* (Turn.) Ag., *S. tortile* (Ag.) Ag., *S. serratifolium* (Ag.) Ag., and *S. macrocarpum* (Ag.) Ag., are retained. He notes the various *Siliquastrum* species of *Halochloa* of Kuetzing's Phycologia generalis as possible synonyms under one or another of the Agardhian species. There is therefore no essential change from C. A. Agardh's disposition, but light is thrown upon the various entities through fuller description and comment. In 1889, however, J. G. Agardh published in the Royal Swedish Academy's "Handlingar" (23: no. 3) his Species Sargassorum Australiae, which, while being particularly devoted to the Australian Sargassums, passed in review all the species of the genus thus far described. He revised and altered to some extent his earlier arrangement within the genus and treated of 143 species, plus about 44 species of doubtful and uncertain nature, or species which ought to be excluded from the genus. To the *Siliquastrum*-assemblage, J. G. Agardh assigned the usual four species and *Sargassum corynecarpum* Harv. (Proc. Am. Acad., 4:328, 1859), while a sixth species of this group, *S. filicinum* Harv. (*loc. cit.,* 327) he placed with *S. Horneri* (Turn.) Ag. and *S. Fengeri* J. Ag. These were all placed under his subgenus III *Bactrophycus,* segregated from his original *Arthrophycus* because of the more typically simple receptacles. J. G. Agardh, however, contributes little in this publication of

1889, except incidentally, toward clearing up the confusion of the *Siliquastrum*-group.

Harvey, as indicated above, added in 1859 (Proc. Am. Acad., 4: 327, 328) two new species to the *Siliquastrum*-complex, *Sargassum filicinum* Harv. and *S. corynecarpum* Harv. *Sargassum filicinum,* as noted earlier, resembles *S. micracanthum* (Kuetz.) Yendo as to vegetative structure. It is diagnosed by Harvey as having thin "leaves," deeply pinnatifid, with the laciniae alternate and bi-tri-dentate at their apices. In addition it has spherical vesicles and siliquaeform receptacles solitary on the apices of the ramuli. In the photograph of the type (earlier spoken of) the habit, texture, etc., are those of Kuetzing's and Yendo's plants. The receptacles are of the antheridial type, elongated and solitary (as often happens in other members of the *Siliquastrum*-group). Yendo (Fuc. Japan, 80, pl. 12, fig. 9) had a few fragments from Misaki which he identified with Harvey's species, and seemingly correctly. The "spherical" vesicle may be matched in other members of the *Siliquastrum*-group, and a terminal, elongated, antheridial receptacle is frequent but not constant.

Sargassum corynecarpum Harv., to judge from a photograph of the type specimen generously contributed many years ago by Professor E. Percival Wright, is a member of the *Siliquastrum*-group, with basal phyllodes, from which arises a main branch which has lost all its phyllodes, including the fulcrants in the inflorescence. Plate 34 shows a similar plant from Hong Kong, but not so completely denuded. Yendo (Fuc. Japan, 81, 84, 1907) refers Harvey's species under *Sargassum serratifolium* (Ag.) Ag. It seems to be a condition of *S. Siliquastrum* (Turn.) Ag., as broadened to include the general assemblage.

In 1907, Yendo (in the Journal of the College of Science, Imperial University of Tokyo, Japan, volume 21, article 12) published his Fucaceae of Japan. This contained detailed studies of the species of the various Fucaceous genera of Japan; among them, studies of *Sargassum.* It is the most important account of the Sargassums of Japan (and of the eastern coast of Asia) published. Detailed illustration is given of the species and their variants, as well as critical discussion. In one respect, however, Yendo's account is disappointing; he fails to describe and discuss, apparently not recognizing their importance, the sex of the receptacles and the sex differentiation among the different species. He speaks hesitatingly of the earlier types which he has not seen, but generally he estimates them logically. He admits *Sargassum filicinum* Harv., *S. serratifolium* (Ag.) Ag., *S. tortile* (Ag.) Ag., and *S. micracanthum*

(Kuetz.) Yendo, as autonomous species. He reduces *S. macrocarpum* Ag. to a variety under *S. tortile* (Ag.) Ag., and he creates *S. Kiushianum* Yendo as a species closely related to *S. micracanthum* (Kuetz.) Yendo. He quotes the other *Siliquastrum* names under one or another of these five, as synonyms of more or less certain status. He separates the *Micracantheae* (*S. micracanthum* and *S. Kiushianum*) from the others of the group on what seem to be inconstant characters and he recognizes the difficulties of strict specific segregation in the general *Siliquastrum*-assemblage. His species have been dealt with earlier in this discussion. A few details only remain to be mentioned. Under *S. serratifolium* (Ag.) Ag. (p. 81) he mentions, as synonym, *Fucus longifolius* Turner, which is very different, as to the specific type, from any of the *Siliquastrum*-group. *Halochloa longifolius* Kuetzing (Bot. Zeit., 1843, 56; Phyc. Gen., 367, 1843; and Tab. Phyc., 10:35, pl. 100, 1860) as indicated by him in the Species Algarum (p. 633, 1849) is (excl. syn.) not the species of Turner, but a variety of *H. serratifolia* (Ag.) Kuetz., and consequently of the *Siliquastrum*-group. Under *S. tortile* (Ag.) Ag. (p. 86) he mentions *Carpacanthus trichophyllus* Kuetz., doubtfully, as a possible synonym, but later (p. 91) he directs attention to Kuetzing's diagnosis and figures (Bot. Zeit., 1843, 57; Phyc. Gen., 368, 1843; Spec. Alg., 622, 1849; Tab. Phyc., 11:12; pl. 37, II, 1861), describing the receptacles as triquetrous with spinose dentate angles, as representing an impossible plant for the Japanese flora and suggesting that the plant "Kuetzing had illustrated was probably a specimen of *S. tortile*, with shrunken receptacles probably angulate." Such shrunken receptacles, simulating the Kuetzing description and figures, certainly do occur in the Hong Kong material of the *Siliquastrum*-assemblage, so that the suggestion of Yendo appears sound. Through the kindness of Dr. Anna Weber-van Bosse, receptacles from the type plant have been examined and the suggestion of Yendo has been verified.

Okamura, in his Icones of Japanese Algae, vol. 5 (1923–1928), has illustrated, described, and discussed *Sargassum serratifolium* (Ag.) Ag., *S. tortile* (Ag.) Ag., *S. micracanthum* (Kuetz.) Yendo, and *S. giganteifolium* Yamada. Okamura has followed the determinations of Yendo, but has added critical remarks. So far as determined, all the *Siliquastrum*-group are dioecious. Yamada directs attention to this fact in connection with his *S. giganteifolium*. This gigantic plant of 2 meters or more in height, with phyllodes up to 22 cm. (8–9 inches) and more pronouncedly paniculate inflorescence, seems to be fairly closely related to the *S. serratifolium*-forms. It is of significance that it fruits in autumn while *S. serratifolium* fruits in spring. It also lacks the characteristically doubly-serrated phyllodes of *S. serratifolium,* and the uppermost phyllodes are coarse and coarsely dentate like the lower, not modified to the extremely skeletonized types characteristic of typical *S. serratifolium* and *S. tortile* plants. In a dried specimen from Enoshima, kindly communicated by Professor Yamada, the oogonial receptacles are undulate or even bluntly toothed. It is probably, however, an extreme ecophene or possibly a gigantic mutant of a tetraploid type. It will be of interest to determine the chromosomic relation between it and other members of the *Siliquastrum*-group.

The final revision of *Sargassum* has come to us as a posthumous contribution from Grunow (Additamenta ad cognitionem Sargassorum). In the first part (Verhandl. d. k. k. zool.-bot. Gesell., in Wien, 65: 329–384, Oct. 1, 1915) where he treats of the *Siliquastrum*-assemblage, he recognizes *Sargassum filicinum* Harv., *S. serratifolium* (Ag.) Ag., *S. tortile* (Ag.) Ag., *S. scoparium* (Turn.) Ag., *S. macrocarpum* Ag., *S. siliquastrum* (Turn.) Ag., *S. corynecarpum* Harv., *S. micracanthum* (Kütz.) Grun. (*sic!*) and *S. Kiushianum* Yendo, with various varieties and synonomy. The other described species of the group are placed in synonomy. Grunow's descriptions, especially of details, and his discussion of the synonomy are most helpful, but he does not attempt to decide critical questions as the list of species admitted as seeming equal shows.

This rather long discussion of the assemblage of species closely related to one another and seemingly possible conditions, states, ecophenes, and possible mutants of *Sargassum Siliquastrum* (Turn.) Ag. has resulted from the attempts to place rather extensive collections of these plants from the Hong Kong region. From consideration of all sources of information, the principal references may, tentatively, be arranged as follows:

Sargassum Siliquastrum (Turn.) Ag.

Species named from fragments—

- *Fucus Siliquastrum* Turner
- *Fucus scoparius* Turner
- *Sargassum macrocarpum* Ag.
- *Sargassum corynecarpum* Harv.
- *Halochloa pachycarpa* Kuetz.
- *Halochloa macracantha* Kuetz.
- *Halochloa polycantha* Kuetz.
- *Halochloa tenuis* Kuetz.
- *Carpanthus trichophyllus* Kuetz.

Ecophenes (?) (types fragmentary)—

- *Fucus tortilis* Ag.
- *Fucus serratifolius* Ag.
- *Sargassum filicinum* Harv.
- *Halochloa micracantha* Kuetz.
- *Sargassum Kiushianum* Yendo

Mutant (tetraploid ?)

- *Sargassum giganteifolium* Yamada

Among the Hong Kong Sargassums there are occasional collections of *Sargassum enerve* Ag., another species which has suffered misinterpretation. *Sargassum enerve* was described by C. A. Agardh (Spec. Alg. 17, 1820) from a specimen of Tilesius, the locality of which is simply designated "in oceano." Agardh compares it with his *S. tortile* and others of the *Siliquastrum*-group. The stem, 2 feet long, is triquetrous to filiform. Its leaves are 1.5 inches long and scarcely 2 lines (4 mm.?) wide, gently and remotely serrate, and entirely ecostate. The vesicles are spherical, often geminate, and mucronate. It seems to have been sterile. A photograph of the type specimen in Herb. Agardh (see pl. 35) shows a narrow-leaved plant and is indicated as a Tilesius specimen, "E mari Coreano," as stated by J. G. Agardh (Spec. Alg., 1:294, 1849). It seems to be exactly the plant sent in by Dr. G. A. C. Herklots from two different localities on opposite sides of Hong Kong Island. It is not the plant figured under the name of *Spongocarpus enervis* by Kuetzing (Tab. Phyc., 10: pl. 89, II, 1860) and referred by J. G. Agardh at first to *Sargassum fulvellum* (Turn.) Ag. and later, but questionably, to *S. enerve* Ag. Yendo (Fuc. Japan, 96, 97, 1907) states that *Sargassum enerve* Ag. and *Spongocarpus enervis* Kuetz. "belong to one and the same species," but *Spongocarpus enervis* Kuetzing (which has elongated vesicles and approaches too closely to *Spongocarpus Horneri* (Turn.) Kuetz.), may be matched for ecostate phyllodes in various specimens of *Sargassum Horneri* (Turn.) Ag. One considerable series of *S. Horneri* in Herb. University of California, collected on the coast of Fukien Province, China, by H. H. Chung, in 1923, shows phyllodes which are entirely ecostate or only abbreviatedly and basally costate. On the other hand, the figure of *Sargassum enerve* published by Kuetzing (Tab. Phyc., II: pl. 13, I, 1861) exactly corresponds to Agardh's type specimen, showing that Kuetzing's *Spongocarpus enervis* is entirely different (as Kuetzing indicates) from *Sargassum enerve* Ag.

For many years there has passed, among the Japanese phycologists (see Yendo, Fuc. Japan, 96, pl. 13, figs. 1–6, 1907, and Okamura, Icon. Jap. Alg., 5:29, pl. 209, 1924), a broad-leaved, large-vesicled plant under the name of *Sargassum enerve* which is entirely different from that represented by the type specimen of C. A. Agardh and delineated in the plate of *S. enerve* of Kuetzing. Okamura (Nippon Sorui Mei, ed. 1, 149, 1902) had earlier identified this as *Sargassum fulvellum* (Turn.) Ag., but Yendo (Fuc. Japan, 98, 1907) considers it distinct and refers under this latter name a plant entirely different (see Fuc. Japan, 92, pl. 13, figs. 18–20, 1907). In 1916, in the second edition of Okamura's Nippon

Sorui Mei, or Enumeration of Algae of Japan, unfortunately for most of us printed in Japanese, Yendo restores *S. fulvellum* (Turn.) Ag. to *S. enerve* Ag. (as a synonym in Okamura, *loc. cit.*, p. 202) and quotes *S. pallidum* (Turn.) Ag., also, as a partial synonym. Yendo also (*in* Okamura, *loc. cit.*, p. 201) gives a new name, *Sargassum Turneri* Yendo, to the *S. fulvellum* Yendo (non *Fucus fulvellus* Turn.) of the Fucaceae of Japan, and he seems wholly justified in doing this.

Fucus fulvellus Turner (Fuci, 1:147, 148, pl. 66, 1808) was founded on a fragment of plant collected by Dr. Horner in the Strait of Corea. The type specimen (see pls. 36 and 37) exists in Herb. Hooker at the Royal Botanic Gardens, Kew, and has been made available for examination through the kindness of the director. A comparison with specimens of *Sargassum enerve* from Japan and with the figures, especially with those of the branches of Okamura's plate 209 (Icon. Jap. Alg., 5: 1905) leaves no doubt as to the identity of the two plants. The Japanese plant should therefore be ranged under *Sargassum fulvellum* (Turn.) Ag. (non *S. enerve* Ag., non *S. enerve* Kuetz., non *Spongocarpus enervis* Kuetz.), while the *Sargassum fulvellum* Yendo (*non* (Turn.) Ag.) should probably be placed under *S. Turneri* Yendo, although this binomial has previously been printed (see J. G. Agardh, Spec. Sarg. Austr., pl. 17, 1889), probably inadvertently for *S. trichophyllum* var. *Turneri* J. Ag. (*loc. cit.*, p. 52).

In connection with the foregoing discussion of the *fulvellum-enerve* confusion, the status of *Fucus pallidus* Turner (Fuci, 1:149, 150, pl. 67, 1808) has become involved. The type specimen (see pls. 43 and 44), through the kindness of the director of the Royal Botanic Gardens at Kew, has been located in Herb. Hooker and made available for examination. It shows oospores only in the receptacles. J. G. Agardh (Spec. Alg., 1:294, 1848) referred it to *Sargassum enerve* Ag. with a "?." Yendo (Fuc. Jap., 109, 1907) discusses the question and is inclined to refer it (as he does with a "?") under *S. confusum* Ag., although he seems to feel that *Halochloa pallida* (Turn.) Kuetz. (Tab. Phyc., 10: pl. 94, II, 1860) is referable rather to *S. piluliferum* (Turn.) Ag. A careful comparison, however, between Turner's plate and Kuetzing's plate shows that the latter has been copied directly from the former, even with very slight adaptation. There is, besides the general resemblances, one very definite character in Turner's plant which is to be found also in Agardh's plant and appears also in Yendo's plant, and that is the cryptostomata on the vesicles. These are found also on the vesicles of *Fucus microceratius* Mertens (*in* Turner, Fuci, 2:152, pl. 130, 1809) whose type, seemingly a much bedraggled specimen and not to be located in Herb. Hooker at Kew, was described from a Horner specimen from the Strait of Corea. This otherwise seems possibly to belong to the group now usually placed under *S. confusum* Ag. Mertens adds little in his later account (Mem. Mus. d'Hist. Nat., Paris, 5:181, 1819) to assist in placing the species. C. A. Agardh (Spec. Alg., 35, 1820) removed it to *Sargassum,* quoting a specimen received from Tilesius. J. G. Agardh (Spec. Alg., 1:295, 1848) keeps it distinct, but places it next to *S. confusum* Ag., an opinion expressed later (Spec. Sarg. Austr., 39, 127, 1889) with a "?." Kuetzing (Spec. Alg., 635, 1849), after seeing a dried specimen, refers the Turner species doubtfully to *Myagropsis.* Grunow (Add. Cog. Sarg., 1:352, 1915) also keeps it distinct, but as of uncertain position, adding that the receptacles are antheridial in the specimen he examined while Turner indicates that they are oogonial. Yendo, however, seems to think that there is some resemblance to *S. piluliferum* (Turn.) Ag. although the vesicles are both apiculate and sparsely dotted with cryptostomata.

After careful study of the situation, although the only type specimen available is that of *Fucus pallidus* Mert., it seems that *Fucus pallidus* Turn., *Fucus microceratius* Mert., and *Sargassum confusum* Ag. are names for one and the same species of the Japanese coasts, whose proper designation must be *Sargassum pallidum* (Turn.) Ag. This species includes under it as undoubted synonyms, *Fucus microceratius* Mertens and *Sargassum confusum* Ag. Somewhat later on, another synonym will be discussed, viz., *Fucus Acinaria* var. *pycnocistus* (Mert.) Turner (Fuci, 1:110, 1808), for which the name *Fucus pycnocistus* Mertens MS is quoted in the synonymy.

The confusion does not, however, end here, but plunges us into still another and less readily resolvable mixture. When describing his *Sargassum confusum,* C. A. Agardh (Syst. Alg., 301, 302, 1824) states that this is the plant he described and included under his earlier (Spec. Alg., 22, 23, 1820) *S. acinaria,* excluding the synonym of Turner and of several collections, as well as the *Fucus heterophyllus* of his Algarum Decas Quarta (no. 32, p. 43, 1815), and also excluding the synonyms of Turner and others. Much obscurity attends the exact identity of both the *Fucus acinarius* L. as interpreted by Turner and *F. heterophyllus* Turner.

Fucus heterophyllus Turner (Fuci, 2:62, pl. 92, 1809) was evidently founded on two plants, the first mentioned being from the coast of Japan, collected by "Sir C. P. Thunberg," the other brought back from the "coast of New Holland" by Robert Brown. Turner states that he "has been unable to find in any author a description of the Fucus here figured," and speaks of "specimens of it" being preserved in the Linnean and Banksian herbaria, as well as in Mr. Brown's splendid collection of the plants of New Holland, and of having received others, through the kindness of Professor Mertens, gathered in Japan by Sir C. P. Thunberg. He goes on to state that the name of *F. heterophyllus* is given to it in the Banksian Herbarium. It seems, therefore, that the type must be looked for in the Banksian Herbarium and that Turner adopted a MS name of Robert Brown. The Japanese plant may be considered to have been included inadvertently, assuming, however, that the type is Australian. Unfortunately, it is not possible at this present writing to explore the Banksian Herbarium to ascertain the possible existence and the exact identity of the supposititious type. C. A. Agardh (Spec. Alg., 1:21, 1820) lists three regions for *Sargassum heterophyllum:* first, Cape of Good Hope; second, Japan; and third, Australia. In the Systema Algarum (p. 301, 1824) he also lists the three regions (or sets of specimens). J. G. Agardh (Spec. Alg., 1: 296, 297, 1848) lists only the Cape of Good Hope and suggests in regard to the Thunberg specimen quoted by Turner, and fortified by fragments sent under the name of *Fucus heterophyllus* and derived from the Thunberg specimen itself, that it seems to belong to *Sargassum Siliquastrum.* A specimen from Herb. Turner (see pl. 38), in Herb. Hooker at Kew, made accessible through the kindness of the director, may have been the original of Turner's plate (Fuci, 2: pl. 92, 1809). It seems to be Mertens's specimen, with notes (seemingly in Mertens's handwriting ? suggesting that it may be the *Fucus lendigerus* L.), and is distinctly labeled "ex Cap. b. Spei. Thunberg." Assuming that this specimen is the plant figured and described by Turner, it becomes necessary to regard the later restriction of *Sargassum heterophyllum* (Turn.) Ag. to the South African plant as correct and to suspect that Turner made a slip of the pen in noting the locality whence it came. The Herb. Banksian plants from Australia and a possible Thunbergian plant of *S. Siliquastrum* from Japan may have been included by Turner, but of the latter there is no evidence before us at present except the statement of J. G. Agardh. If *S. heterophyllum* is to be included in the flora of the eastern Asiatic coast, it can be only as a *pro parte* synonym and probably under *S. Siliquastrum* (Turn.) Ag.

The history of *Sargassum acinarium* (L.) Ag. (there seems to be no reason for keeping the form *Acinaria*) is both longer and more complex. The original *Fucus acinarius* (*sic!*) L. (Spec. Pl., 2:1160, 1753) was assigned first to the Italian coast and only second to the "Oceano Australiori." The significant citation is to the *Acinaria* of Donati (Essai sur l'hist. nat. de la Mer Adriat., 33, pl. 5, fig. 1, 1758). This remained unchanged in the second edition (Spec. Pl., 2 :1628, 1763). Attention may be directed to the fact that Linnaeus wrote the species name as the ordinary adjective "*acinarius,*" not the generic "*Acinaria*" of Donati. The facts seem evident that Linnaeus cited Donati's figure of the Mediterranean plant and quoted the Italian coast and that he had the common Mediterranean plant in mind, whatever his herbarium may contain to represent it. It is this plant, long and universally known as *Sargassum linifolium* (Turn.) Ag., which should bear the name *S. acinarium* (L.) Ag. (excl. synonymy other than of Linnaeus).

Our present custom with regard to the application of the name began with Turner (Fuci, 1 :110, pl. 49, 1808), who wrote the name *Fucus Acinaria* L. and excluded all the "synonyms" of Linnaeus. Turner explains that he has relied upon the herbarium of Linnaeus rather than upon his writings. There is, at present in the Linnean Herbarium, a single sheet with two unlike specimens, labeled only "*acinarius,*" but without any data as to locality or preference. Through the kindness of the secretary of the Linnean Society of London, a photograph was obtained of this sheet, which, according to Benjamin Daydon Jackson (Index Linn. Herb., 76, 1912), was first authenticated by Linnaeus in 1767, the year of the issue of the second volume of the twelfth edition of the Systema Naturae. There seems to be no certainty as to these plants being the types of the *Fucus acinarius* L. of the first edition of the Species Plantarum of 1753. From the photograph (see pl. 39) it appears that the right-hand plant on the sheet must have been selected by Turner as the type, since its leaves are long and narrow, but the figure of Turner (Fuci, 1 : pl. 49, fig. *e,* 1808) seems certainly indicated, from his drawings both of the leaves and of the bladders, as coming from the left-hand specimen. This, however, he calls var. *β* of Linnaeus, since two scraps in Herb. Turner are also so labeled and as from Herb. Linnaeus. While it is difficult to determine details from a photograph of the right-hand specimen on the Linnaean sheet, it does not seem probable that Turner had the drawing made for his plate 49 from it. In the photograph, there is an appearance of roughness on the axis as if it may be muriculate, but only by a careful examination of the specimen itself can it be ascertained whether, after all, as may be suspected, the right-hand Linnaean specimen may be a rather narrow-leaved form of the Mediterranean species, *S. linifolium* (Turn.) Ag., which Linnaeus undoubtedly had in mind when he founded his *Fucus acinarius,* and to which, despite Turner's scruples, the name of *Sargassum acinarium* undoubtedly belongs.

A search has been made through the Turner specimens in Herb. Hooker, at Kew, to determine if possible the original of plate 49, the *Fucus Acinaria* of Turner, with the result that nothing has been found so definitely labeled as to make it certain. As was said earlier, it seems fairly clear from the photographs of the Linnaean specimens that neither of these can have been used for that purpose. It is certainly not on the sheet containing the Linnaean fragment of var. β (see pl. 45). On this sheet, besides the two Linnaean fragments of var. β (top center) is a specimen (upper left corner) labeled "*F. acinaria* var. ? Egypt. Sir J. Banks," which seems to be what is known as *Sargassum linifolium* var. *Donati* (Kuetz.) Grun.; two others (middle right) labeled "Egypt. Sir Banks 1806," which certainly seem to be *S. linifolium* (Turn.) Ag., included by Turner under *Fucus Acinaria* (Fuci, 1:110, 1808), while the remaining specimen, the largest of all, labeled "F. Acinaria β Hist. Fuc., pl. 49, no. 5, e mari Coreano," is the *Fucus pycnocistus* Mertens MS named by Turner *Fucus Acinaria* var. *pycnocistus* (*loc. cit.*). This specimen (see pl. 45) is not improbably a plant of the same collection used by C. A. Agardh in founding his *S. confusum* (Syst. Alg., 301, 1824). It seems certainly to be *Sargassum pallidum* (Turn.) Ag. Later in the same volume (Fuci, 1: pl. 67, 1808), the species was described as *Fucus pallidus* Turn., an earlier name than *Sargassum confusum* Ag. (1824), but the earliest name is the non-available MS name of Mertens, *Fucus pycnocistus* Mert.

There is, however, a Turner sheet (see pl. 40) which comes under very serious suspicion of being the original of Turner's figure of *Fucus Acinaria.* It is an antheridial plant labeled "Herb. Turner, var. of *F. Swartzii?*" It has the elongated, entire leaves and the characteristic numerous, long, winged, petioled vesicles of Turner's plant, but these also belong to Turner's *Fucus Swartzii* (Fuci, 4:120, pl. 248, 1819) except that the vesicles of this latter species are more apiculate and the leaves somewhat broader and serrate. This corresponds to Grunow's *Sargassum Acinaria* var. *crassiuscula* (Add. Cog. Sarg., (4) 155, 1916). The figure of *Sargassum Acinaria* of Kuetzing (Tab. Phyc., 11: pl. 17, II, 1861) from the Corean Sea (*loc. cit.*, p. 6) seems to agree well with Turner's figure of the larger plant and its parts, and agrees well with specimens collected by the writer at Repulse Bay, Hong Kong Island. In large plants, the upper portions may have the leaves with entire margins, rather thickened and corresponding to the var. *crassiuscula* Grun., while the lower portions have the somewhat thinner, denticulate leaves of typical *Sargassum Swartzii* (Turn.) Ag. (see Turner, Fuci, 4: pl. 248, 1819). The Hong Kong plants ascribed to *S. Swartzii* (Turn.) Ag. and the var. *crassiuscula* (Grun.) comb. nov. have the receptacles smooth to somewhat spiny at the tips, so that a certain amount of spiny character may be assumed, safely, for both the species and the variety, as well as for *S. acinaciforme* Mont.

Of the var γ *megalocarpus* of Turner's *Fucus Acinaria,* said to have come from the Red Sea, collected by Viscount Valentia, no specimen so designated has been located. It is distinguished by having "receptacles oblong, undulated, spinous," and recalls the Red Sea *Sargassum acinaciforme* Mont. (Ann. Sci. Nat., ser. 3, 13 :1849), whose receptacles, however, are described as *not* being spiny. Since, however, in the Hong Kong specimen some receptacles are slightly "spinous" at the apex, this may be true, also, of *S. acinaciforme* Mont. There is a Turner sheet in Herb. Hooker, without locality or date, and marked simply "curious var. of *F. Acinaria,* Herb. Turner" (see pl. 41), which seems to be *S. acinaciforme* Mont. on account of its resemblance to Kuetzing's representation of a Montagne specimen (see Tab. Phyc., 11 :9, pl. 29, 1861). This may be suspected of being one of the original Red Sea specimens, although the receptacles are not well developed.

The type (see pl. 42) of *Fucus Swartzii* Turner (Fuci, 4 :120, pl. 248, 1819) described from a specimen whose locality was unknown, but sent to Turner by Dr. Olof Swartz, so well known from his work on West Indian Botany and on many families of flowering plants as well as on mosses and ferns among the Cryptogams, is readily to be identified among Turner's specimens in Herb. Hooker at Kew. It represents the lower part of a main branch and seems to be only a portion of the plant drawn for Turner's plate. The specimen is indicated by the label "*F. Swartzii,* Dr. Olof Swartz," and was probably a bit out of some miscellaneous collection sent to Swartz. The receptacles seem immature and likely to be antheridial. They are smooth. The correspondence between this plant and the Hong Kong specimens previously mentioned is very close. The Hong Kong region may be the original source of this species, but its distribution may be broader, even to Hindustan on the one hand and north Australia on the other, but the question as to the relation of *Sargassum Swartzii* (Turn.) Ag. to *S. acutifolium* Greville (Ann. and Mag. Nat. Hist., ser. 2, 3 :256, pl. 10, 1849) remains to be solved. There is a close resemblance, as Greville has noted that "it is not without considerable hesitation that I separate this plant from *Sargassum acinaria* of Agardh" (taking *Fucus Acinaria* Turn. as type). Greville's plant seems to have much more acute leaves than any form of *S. Swartzii* (Turn.) Ag. It may, however, be only the upper part of an oogonial plant of *S. Swartzii* (Turn.) Ag. (*Fucus Acinaria* Turner as to type, not of Linnaeus).

While this discussion has extended to greater length than was expected, there is one other east Asiatic species to be discussed, and that is *Sargassum fuliginosum* Kuetzing (Spec. Alg., 612, 1849; Tab. Phyc., 11:6, pl. 19, I, 1861), said to have been collected in Kamtschatka by Horner, a specimen communicated to Kuetzing by Shuttleworth. J. G. Agardh (Spec. Sarg. Austr., 127, 1889) mentions it among the uncertain species of the Racemosae, but does not attempt to place it more definitely. Grunow (Add. Cog. Sarg., (4) : 172, 1916) keeps it separate from *S. filipendula* Ag., from which he thinks it to be distinguished chiefly by its widely separated locality. J. G. Agardh (Anal. Alg., Cont. III, 60, 1896) refers to it a Japanese specimen collected by Kjellman. Yendo (Fuc. Jap., 106, 110, 1907) places it doubtfully under *S. confusum* Ag., but considers it to be a very uncertain form, especially since it is extremely doubtful that any Sargassums live on the coast of Kamtschatka proper; he thinks that it comes near to *S. confusum* Ag. As stated earlier in this discussion, the long-petioled, non-dotted vesicles, the siliquose racemed receptacles, and the narrow, almost entire leaves, together with the general habit, prevent its being placed under or even near *S. confusum* Ag. (*S. pallidum* (Turn.) Ag.), but do suggest very strongly Hong Kong plants of the relationship of *Sargassum Henslowianum* Ag. (see J. G. Agardh, spec. Sarg., Austr., pl. 11, 1889) and, in particular, the variety (or form? or state?) of that species named by Grunow (Add. Cog. Sarg., (4) :176, 1816) *S. Henslowianum* var. *Bellonae*.

EXPLANATION OF PLATES

PLATE 26

1. *Codium decorticatum* (Woodw.) M. A. Howe.
   Type specimen in Herb. Kew.
2. *Codium elongatum* C. Ag.
   Type specimen in Herb. Agardh, University of Lund, Sweden. × 0.5.

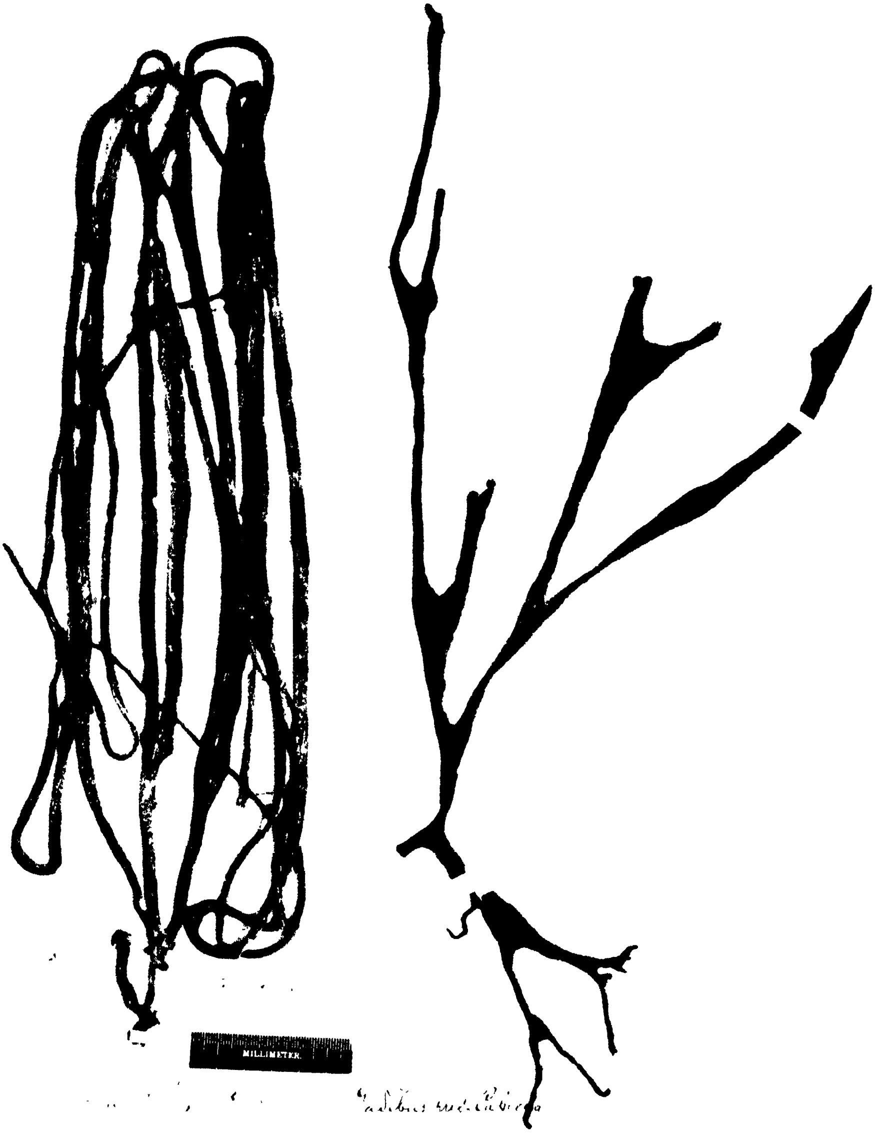
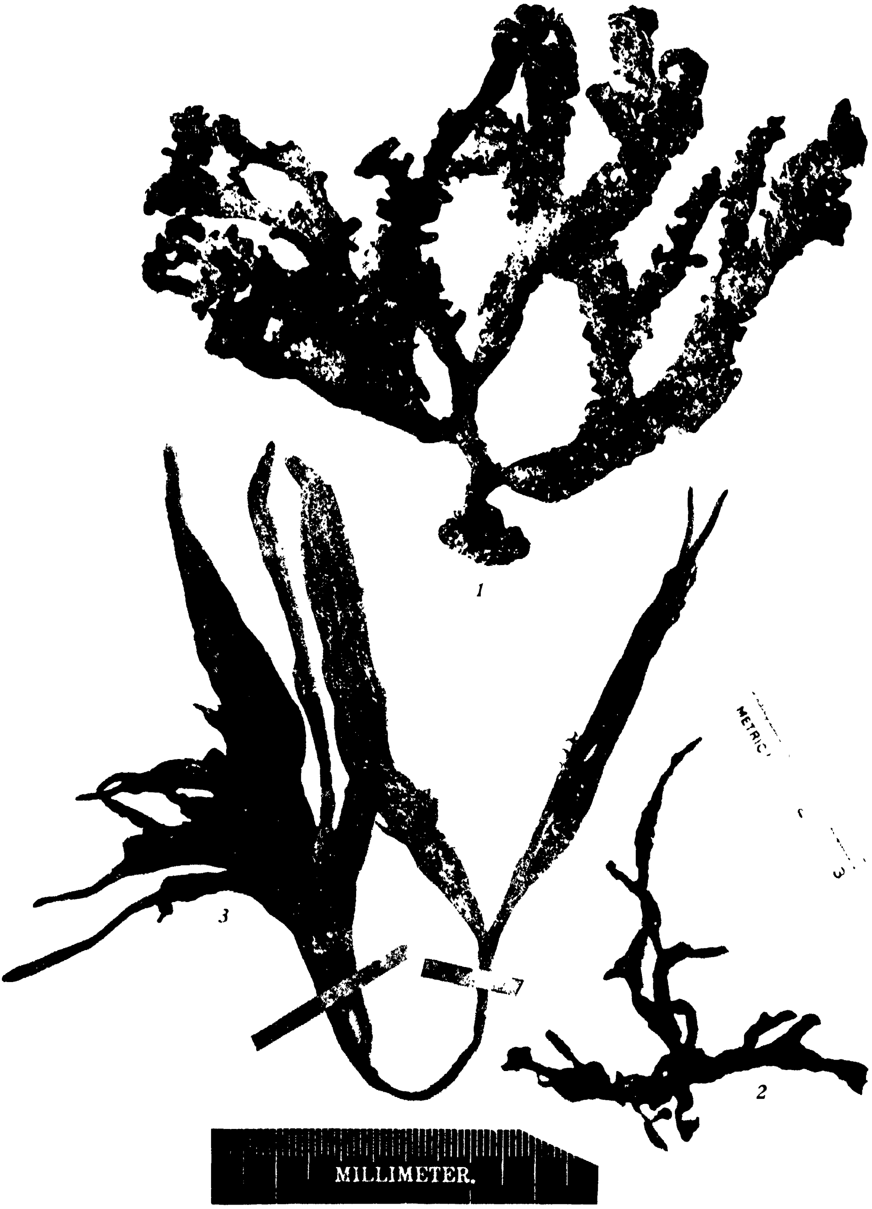

MILLIMETER.

PLATE 27

1. *Codium lineare* Ag.
   Type specimen in Herb. Agardh, University of Lund, Sweden. × 2.
2. *Codium decumbens* Martius.
   Cotype, Staats Herbarium, Munich.
3. *Codium decumbens* Martius.
   Glaziou, no. 2445, Rio de Janeiro, in Herb. Martius.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MILLIMETER.

PLATE 28

Codium decumbens Martius.
Uruguay (Herb. Univ. Calif., no. 341344).

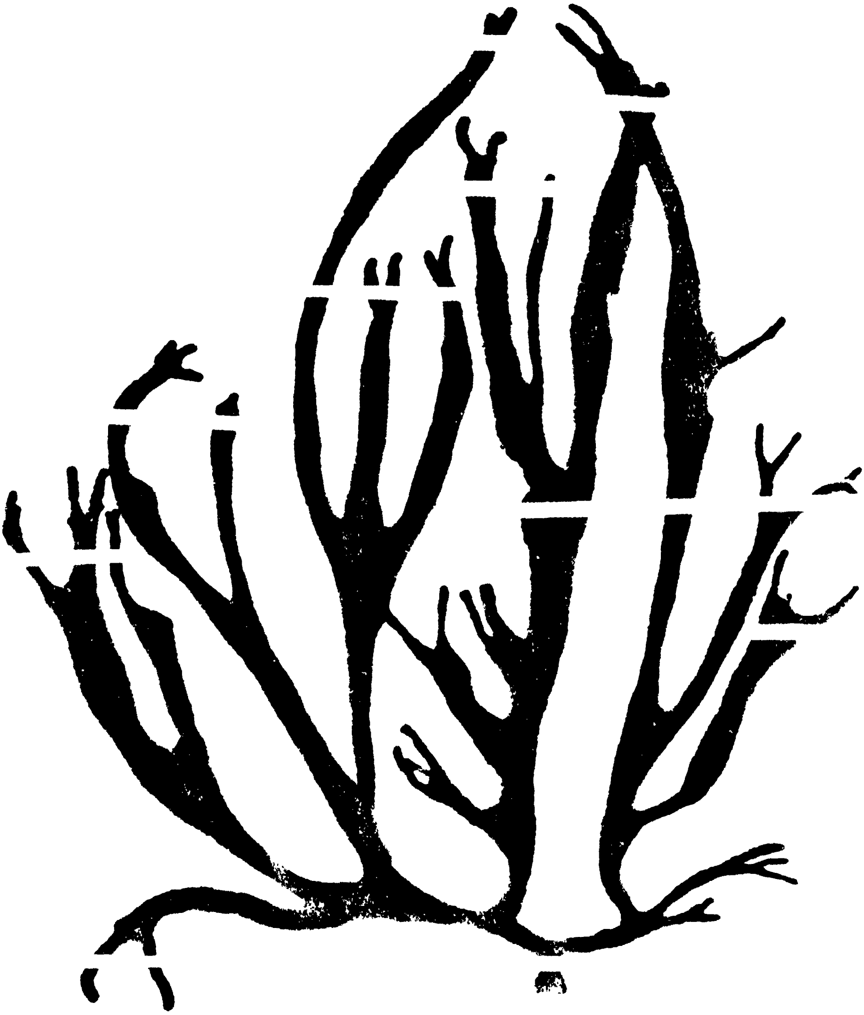


PLATE 29

1. Utricle of type of *Codium decorticatum* (Woodw.) M. A. Howe. × 95 diam.
2. Utricle of type of *Codium elongatum* Ag. × 95 diam.
3. Utricle of type of *Codium lineare* Ag. × 95 diam.

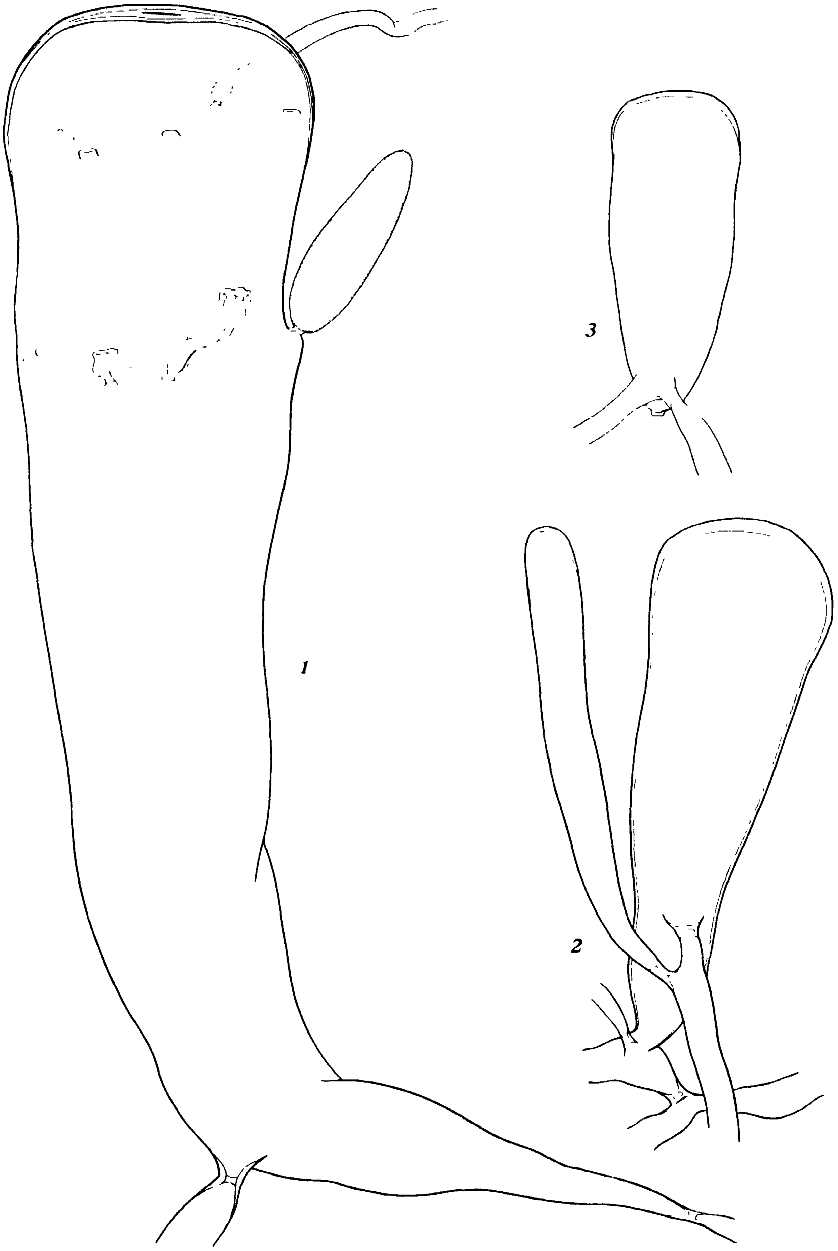


PLATE 30

Codium decumbens Martius.
Utricles of Uruguay specimen. × 95 diam.

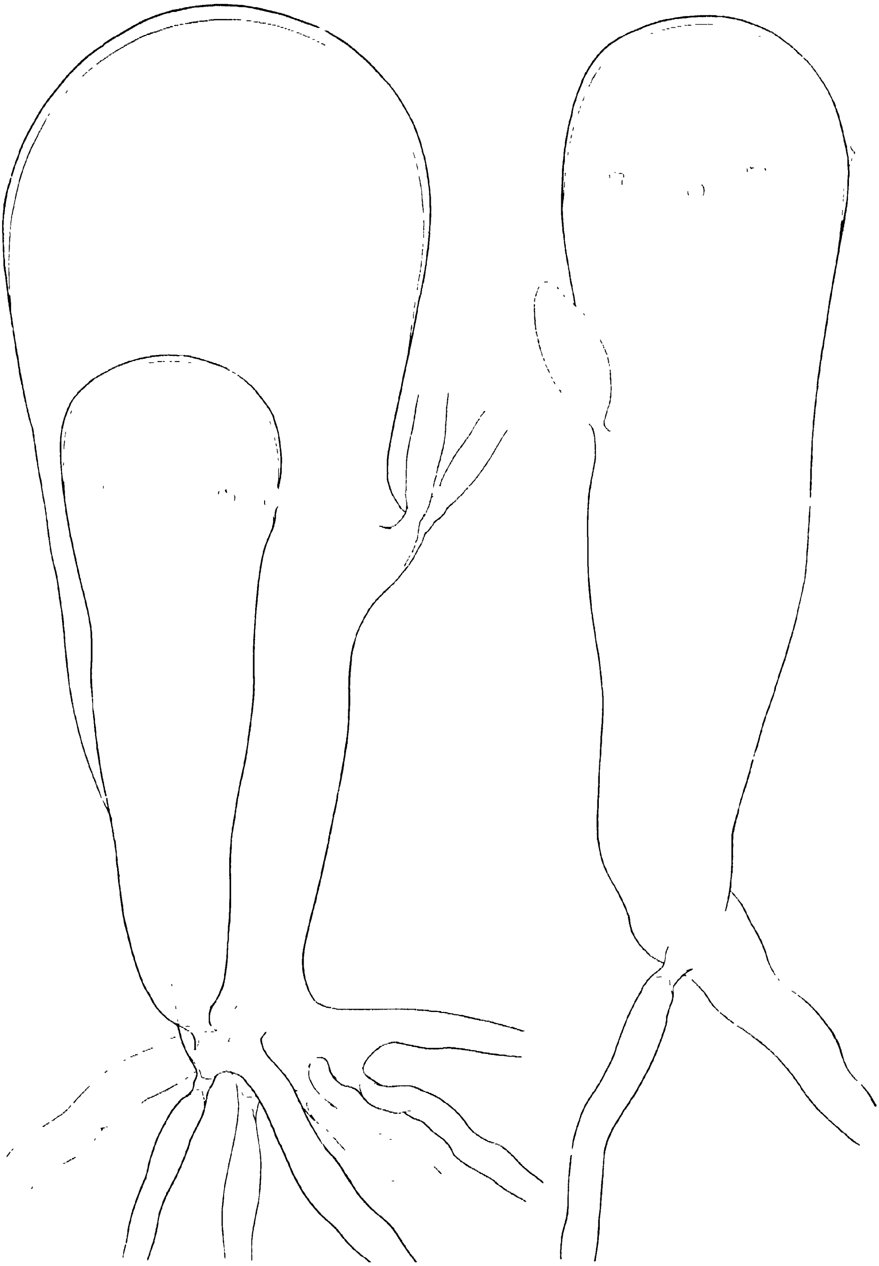


PLATE 31

Sargassum Siliquastrum (Turn.) Ag.

Hong Kong specimen, simulating *Fucus Siliquastrum* Turner (Herb. Univ. Calif., no. 482582).

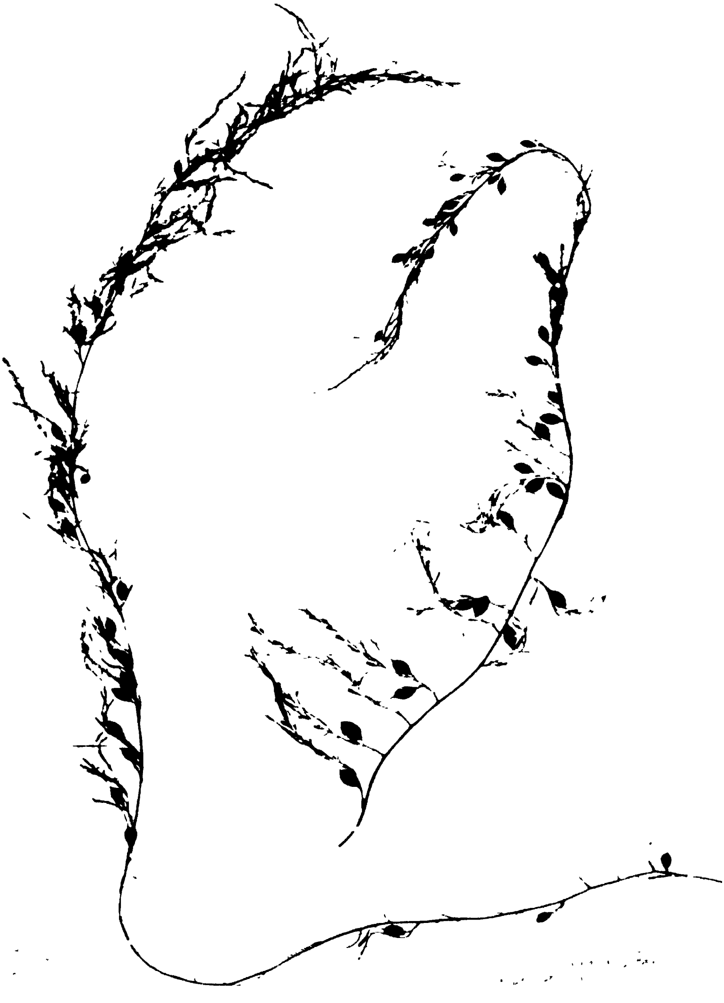


PLATE 32

Sargassum Siliquastrum (Turn.) Ag.

Hong Kong specimen, simulating *Fucus scoparius* Turner (Herb. Univ. Calif., no. 482537).

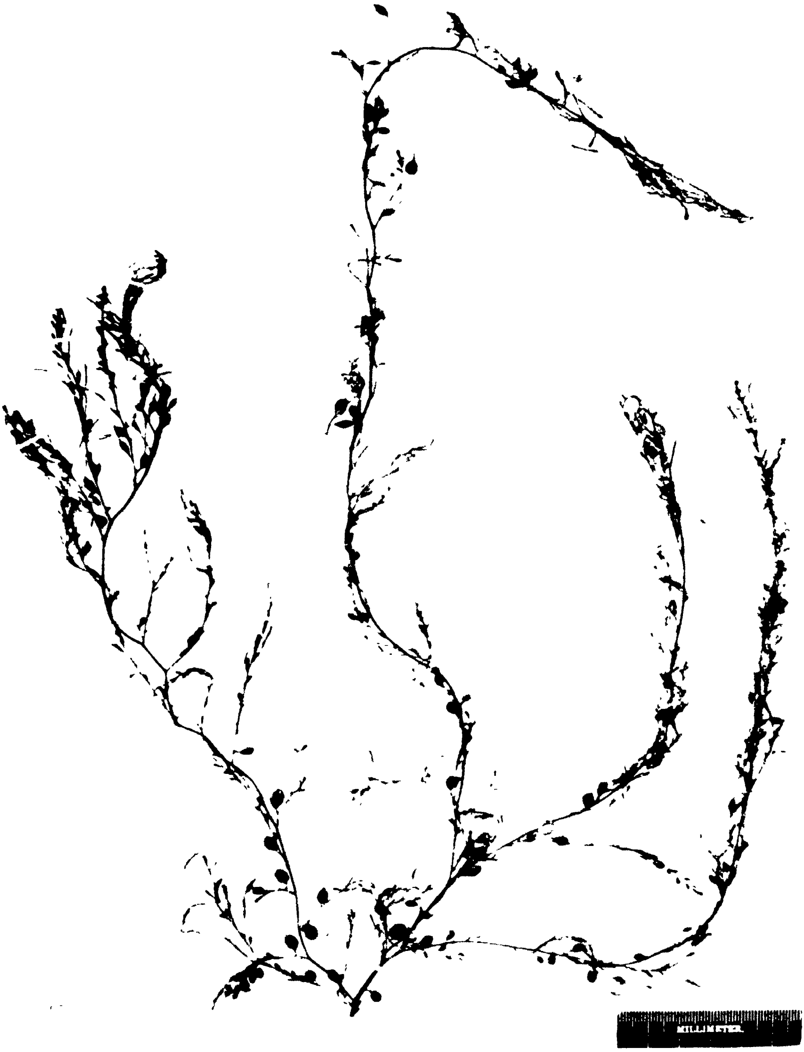

MILLIMETER

PLATE 33

Sargassum Siliquastrum (Turn.) Ag.

Hong Kong specimen, simulating *Sargassum macrocarpum* Ag. (Herb. Univ. Calif., no. 482573).

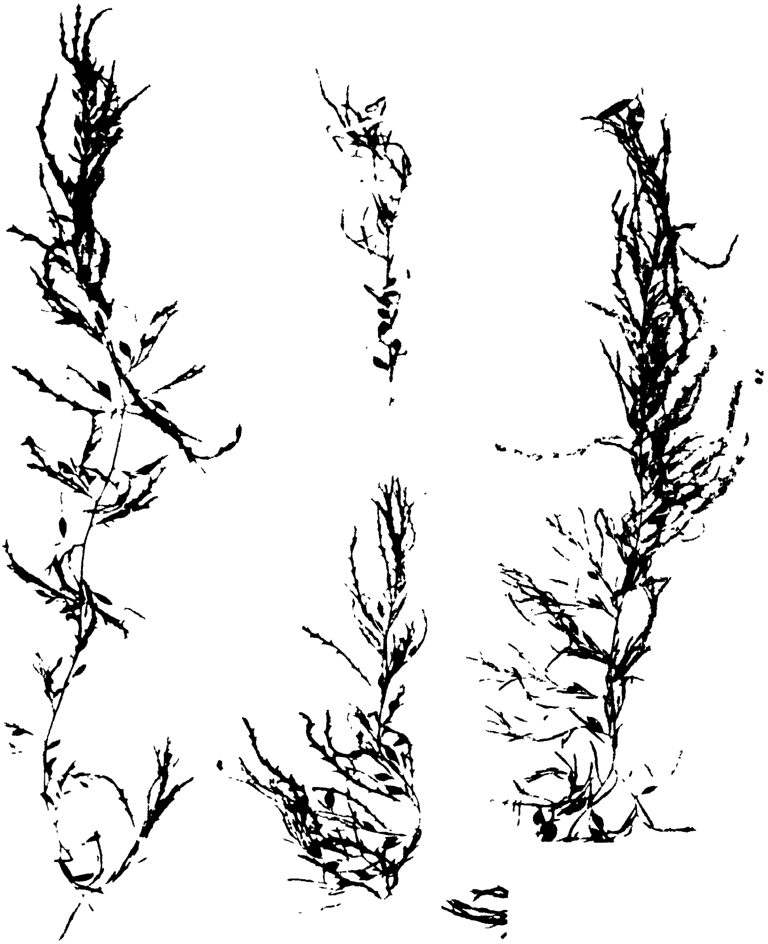


PLATE 34

Sargassum Siliquastrum (Turn.) Ag.
Hong Kong specimen, simulating *Sargassum corynecarpum* Harv. (Herb. Univ. Calif., no. 482589).

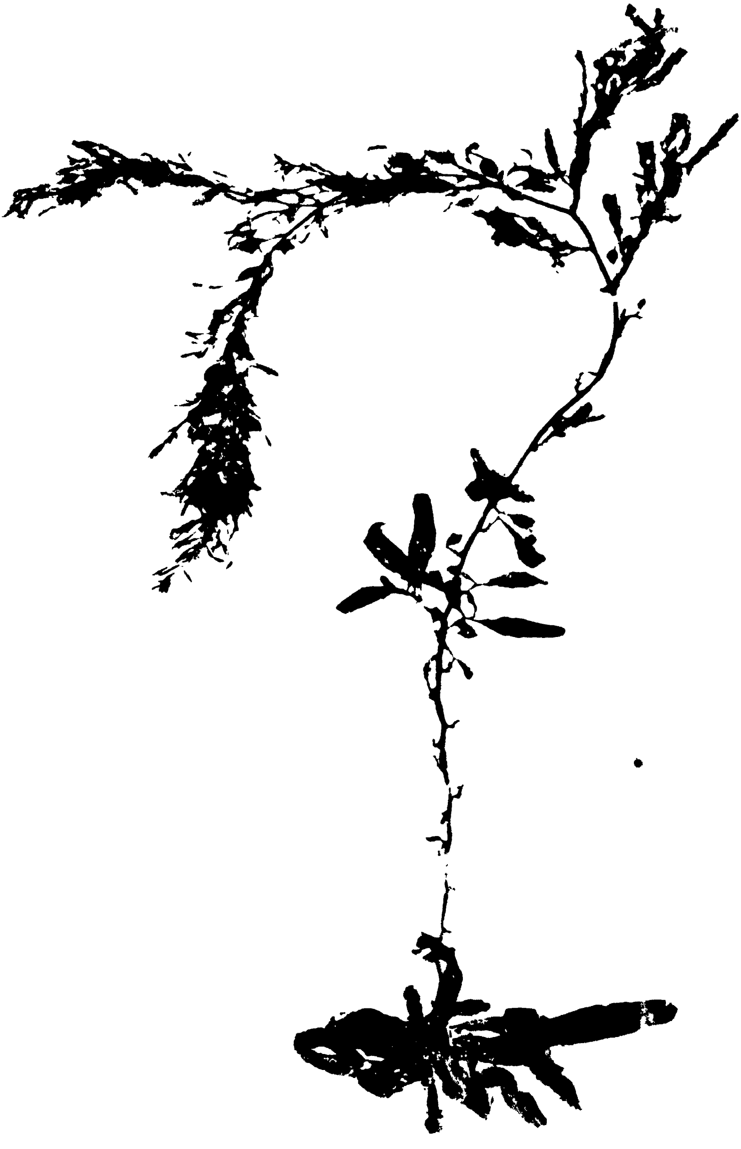
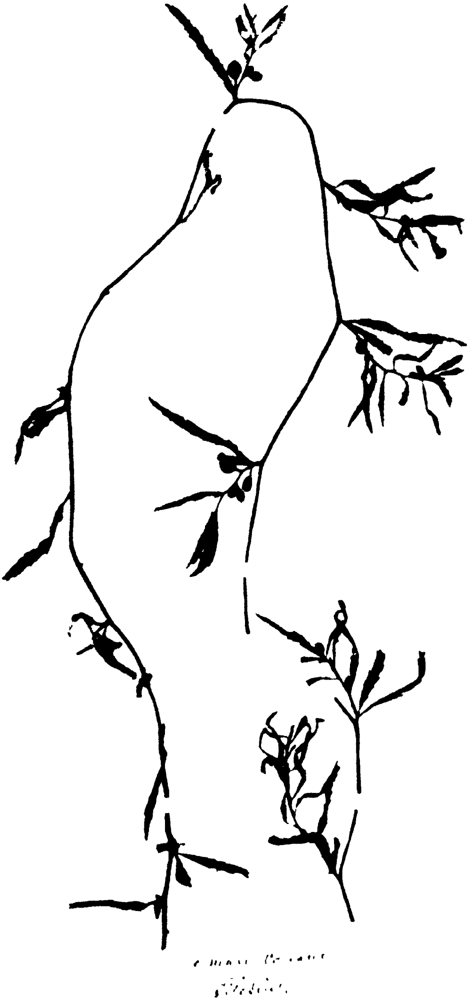


PLATE 35

Sargassum enerve Ag.

Type sheet from Herb. Agardh, at the University of Lund, Sweden.



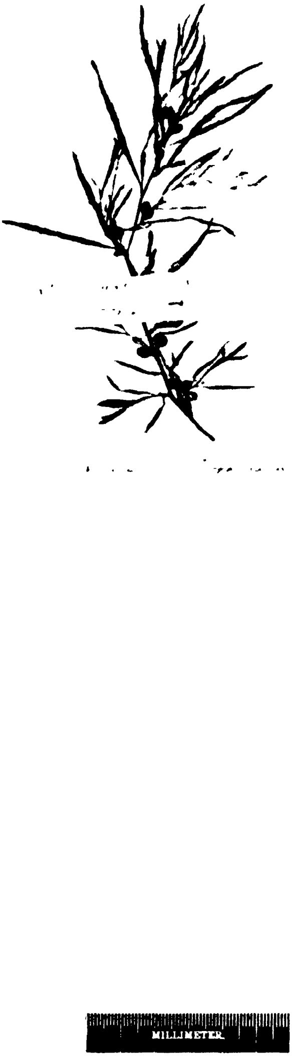

MILLIMETER

PLATE 36

Sargassum fulvellum (Turn.) Ag.
Type specimen of *Fucus fulvellus* Turner in Herb. Kew.

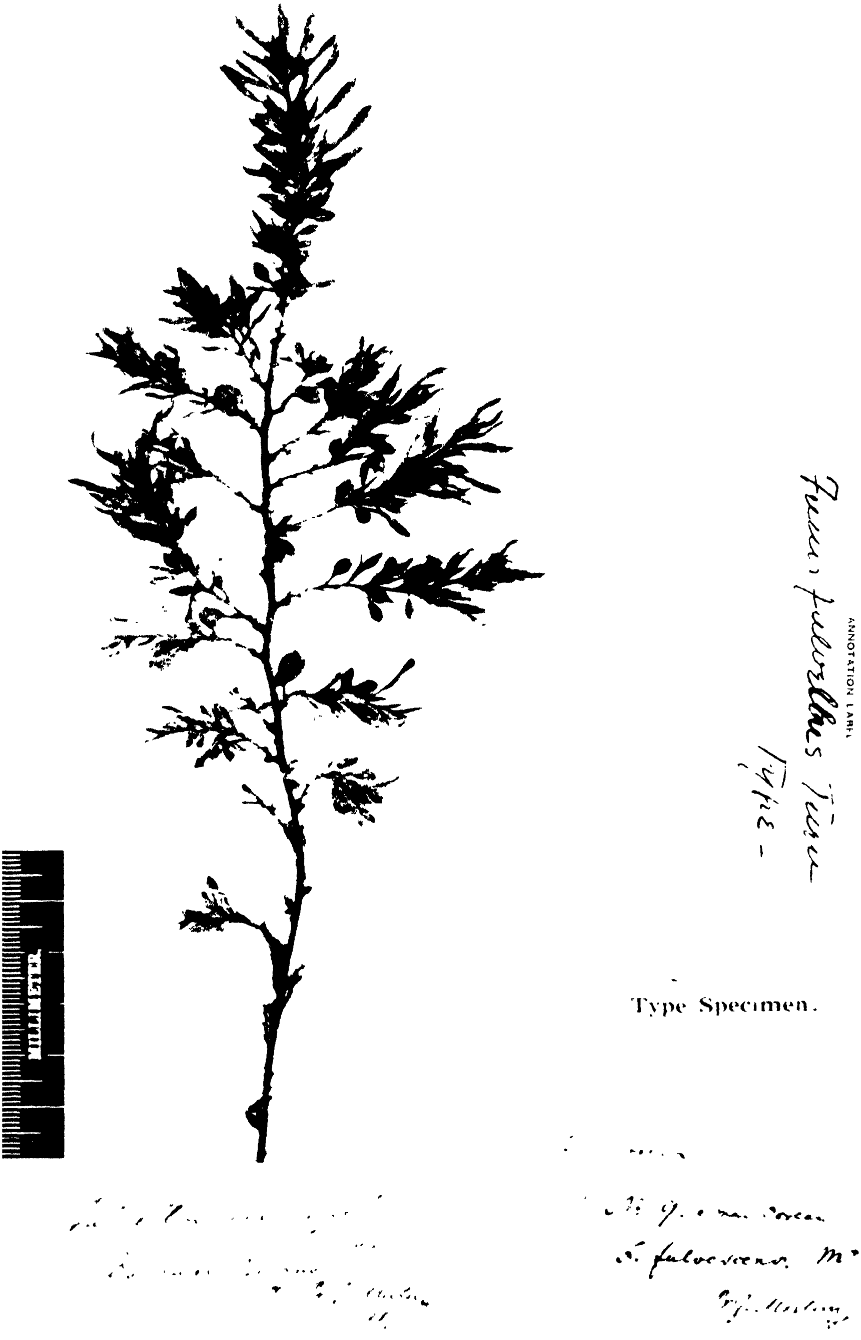

ANNOTATION LABEL
Fucus fulvellus Turner
Type -
Type Specimen.
S. fulvescens

PLATE 37

Sargassum fulvellum (Turn.) Ag.

Portion of type specimen of *Fucus fulvellus* Turn., magnified × 5 diam.

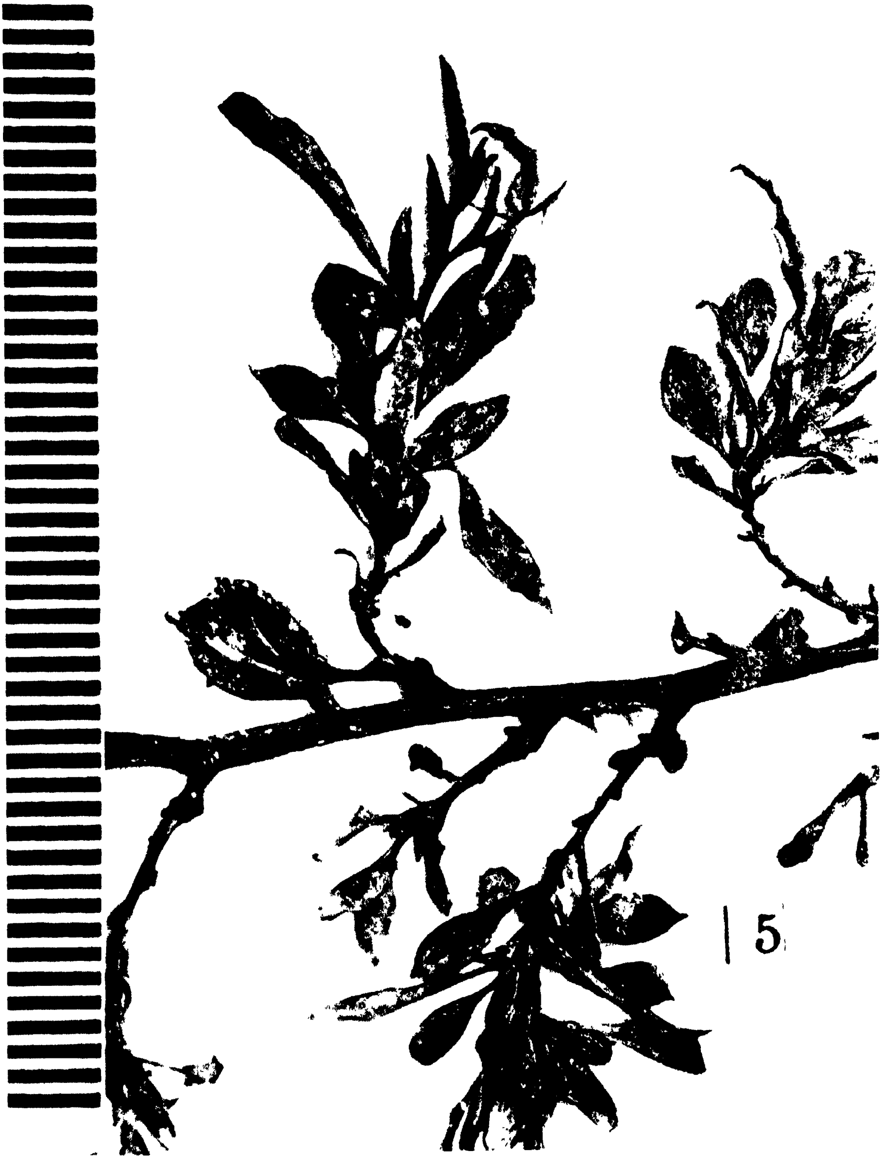

5

PLATE 38

Sargassum heterophyllum (Turn.) Ag.
Type (?) specimen of *Fucus heterophyllus* Turner in Herb. Kew.

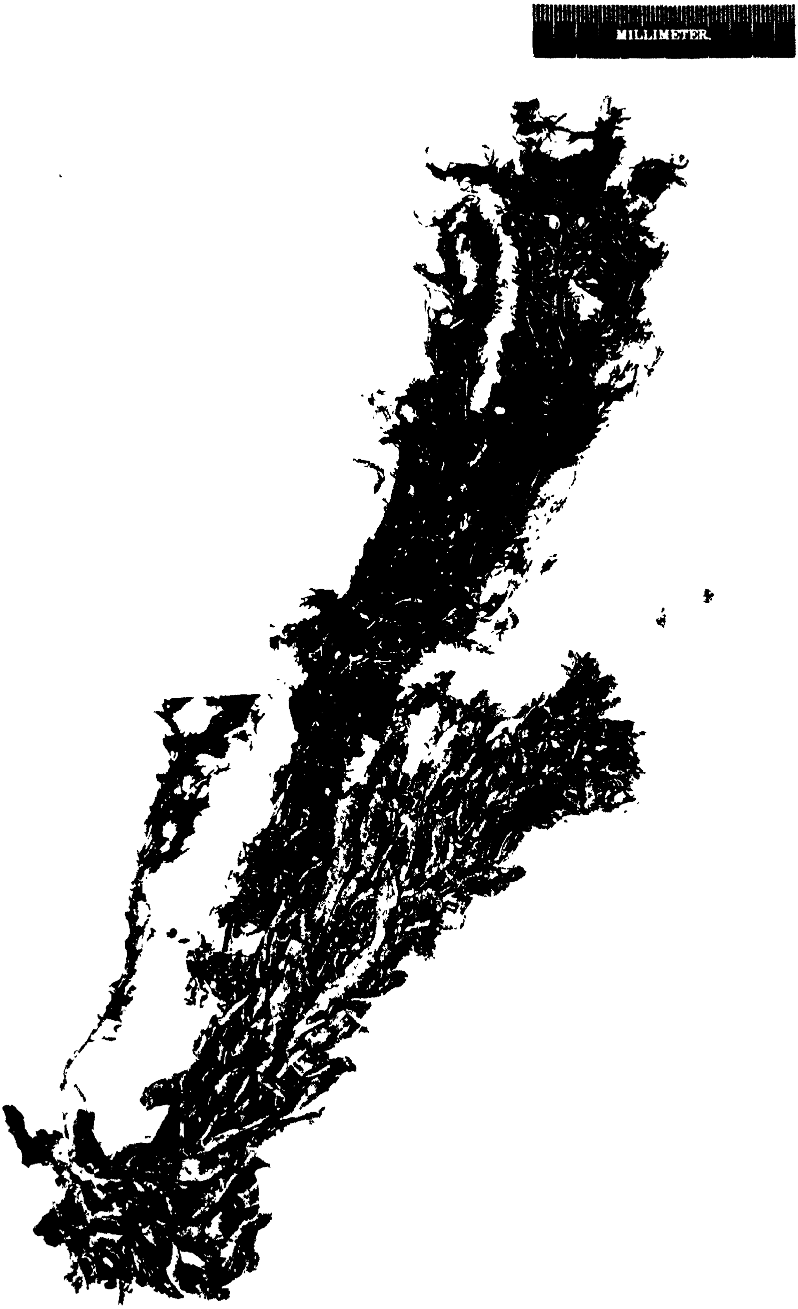
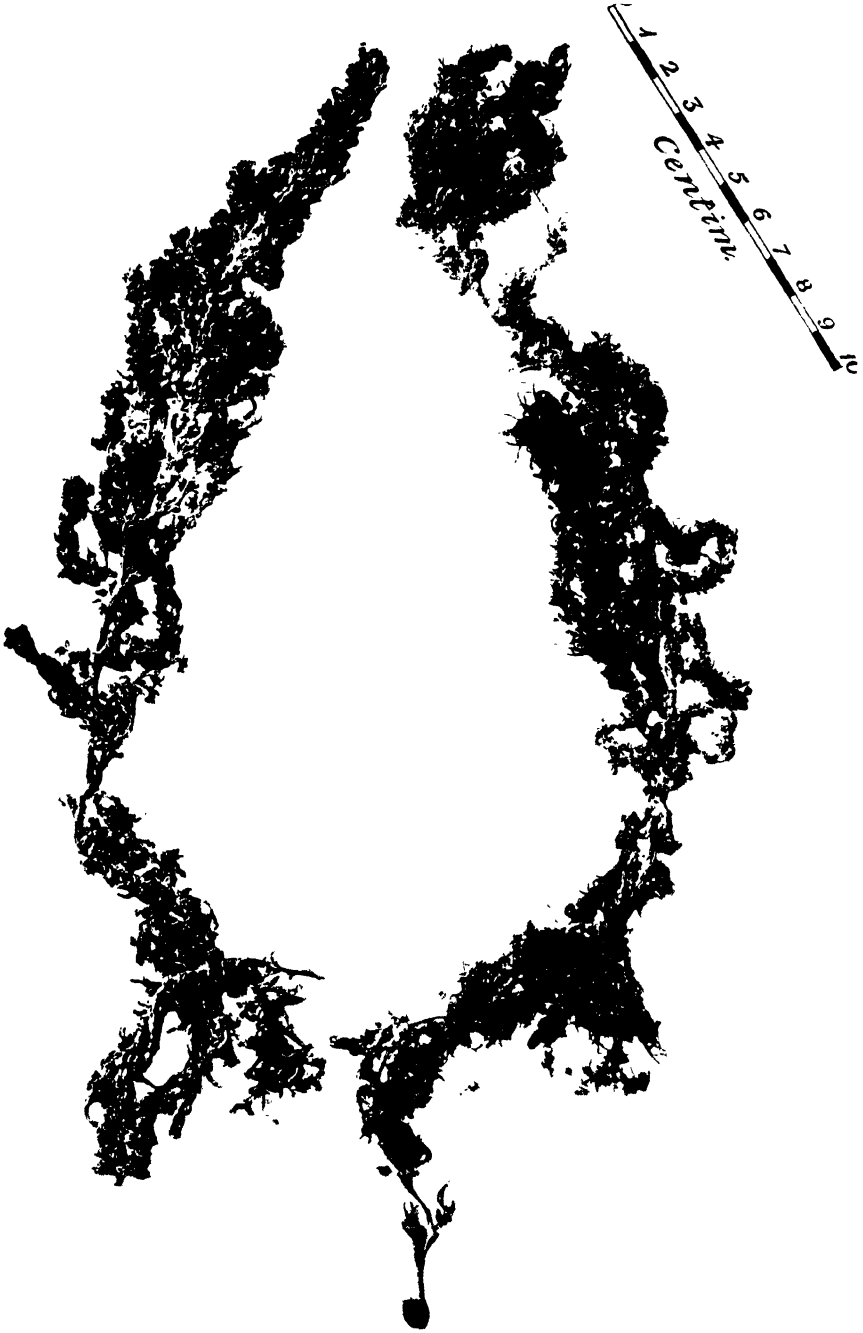

MILLIMETER.

PLATE 39

Fucus acinarius L.
Type sheet in the Linnean Herbarium, London.


1
2
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Centim.

PLATE 40

Sargassum Swartzii (Turn.) Ag., var *crassiuscula* Grun.
Type (?) sheet of *Fucus Acinaria* Turner (*non* Linnaeus) in Herb. Kew.

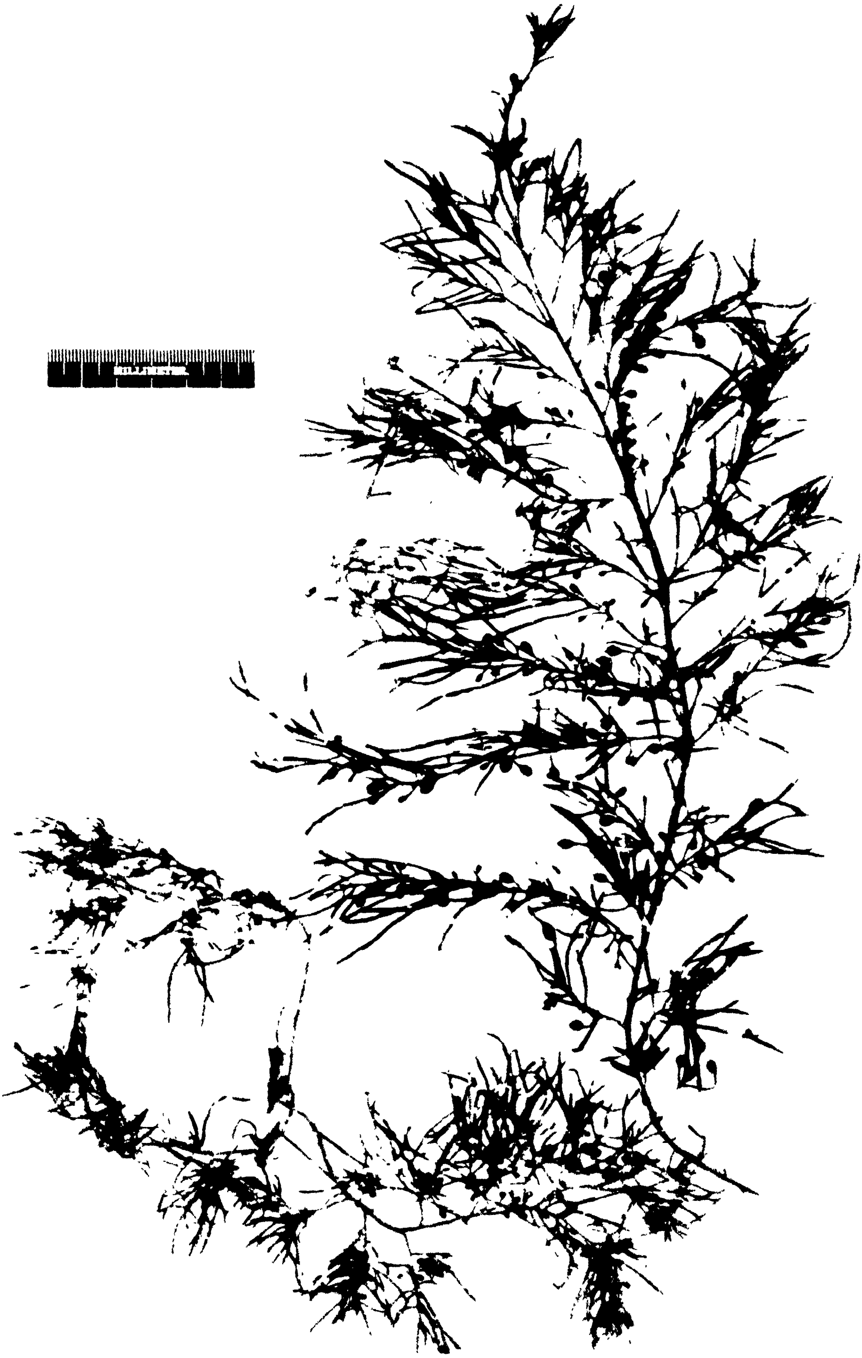


PLATE 41

Sargassum acinaciforme Mont.

Sheet of Turner specimens from Herb. Kew, suspected of being *Fucus Acinaria* var. *megalocarpus* Turner.

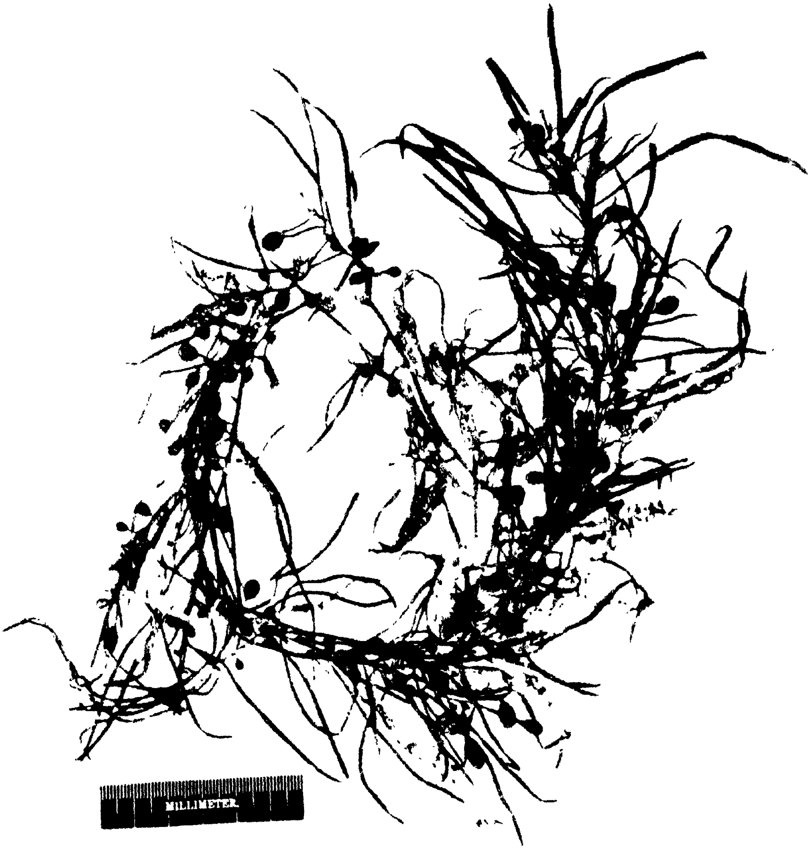
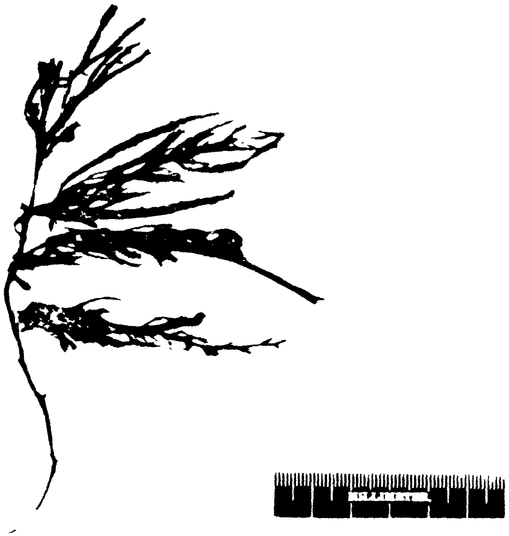
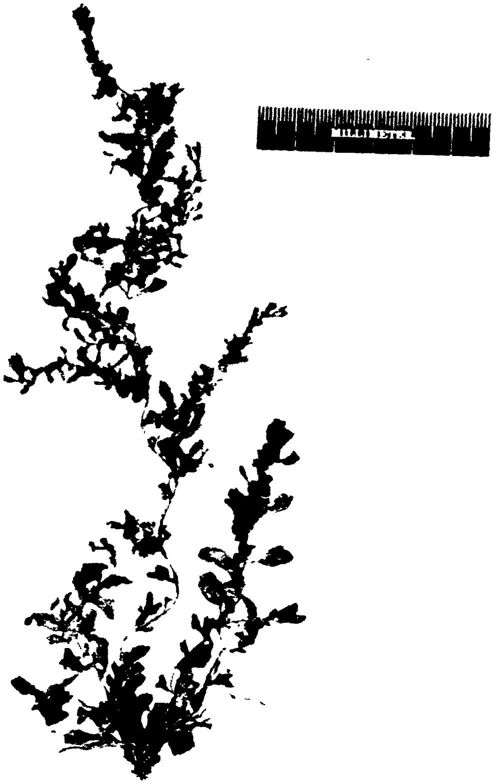

MILLIMETER.

PLATE 42

Sargassum Swartzii (Turn.) Ag.
Type specimen of *Fucus Swartzii* Turner, in Herb. Kew (lower specimen).



MILLIMETER



MILLIMETER

PLATE 43

Sargassum pallidum (Turn.) Ag.
Type specimen of *Fucus pallidus* Turner in Herb. Kew.

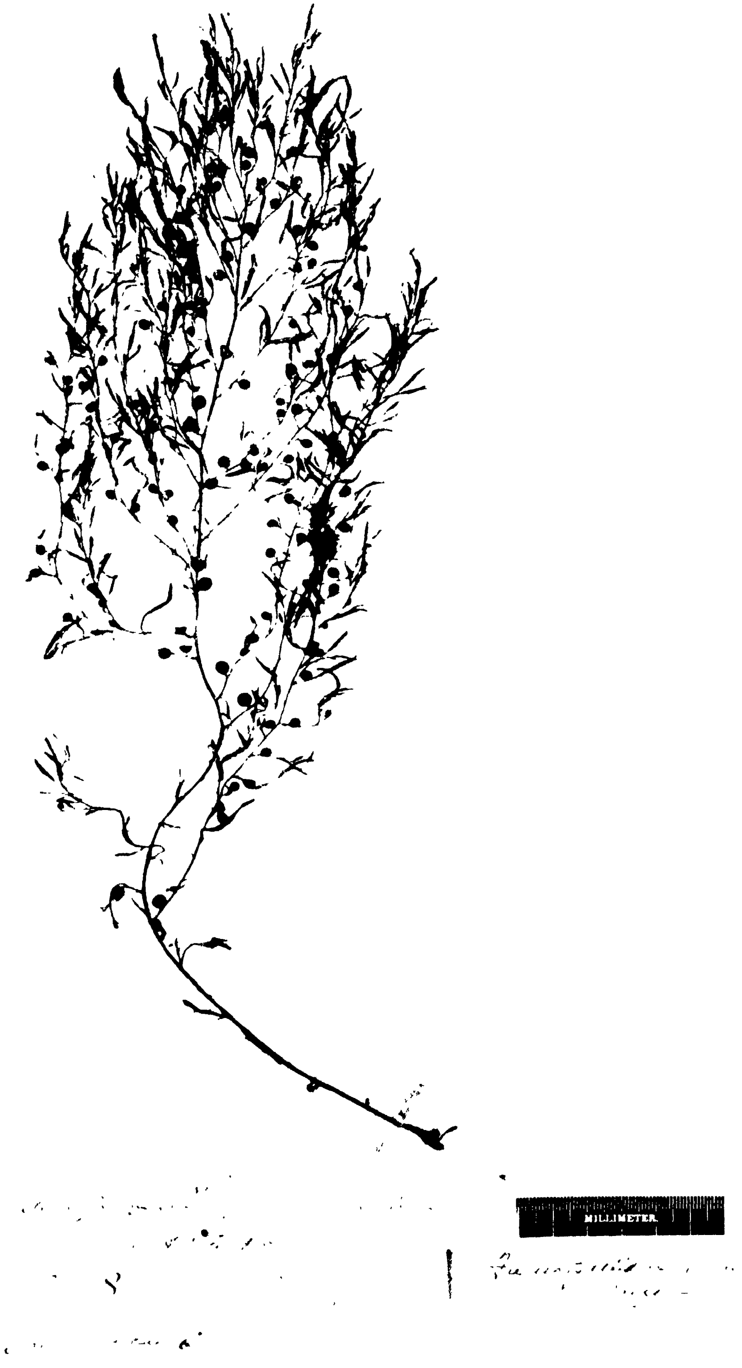

MILLIMETER

PLATE 44

Sargassum pallidum (Turn.) Ag.

Portion of type specimen of *Fucus pallidus* Turner, enlarged × 5 diam.

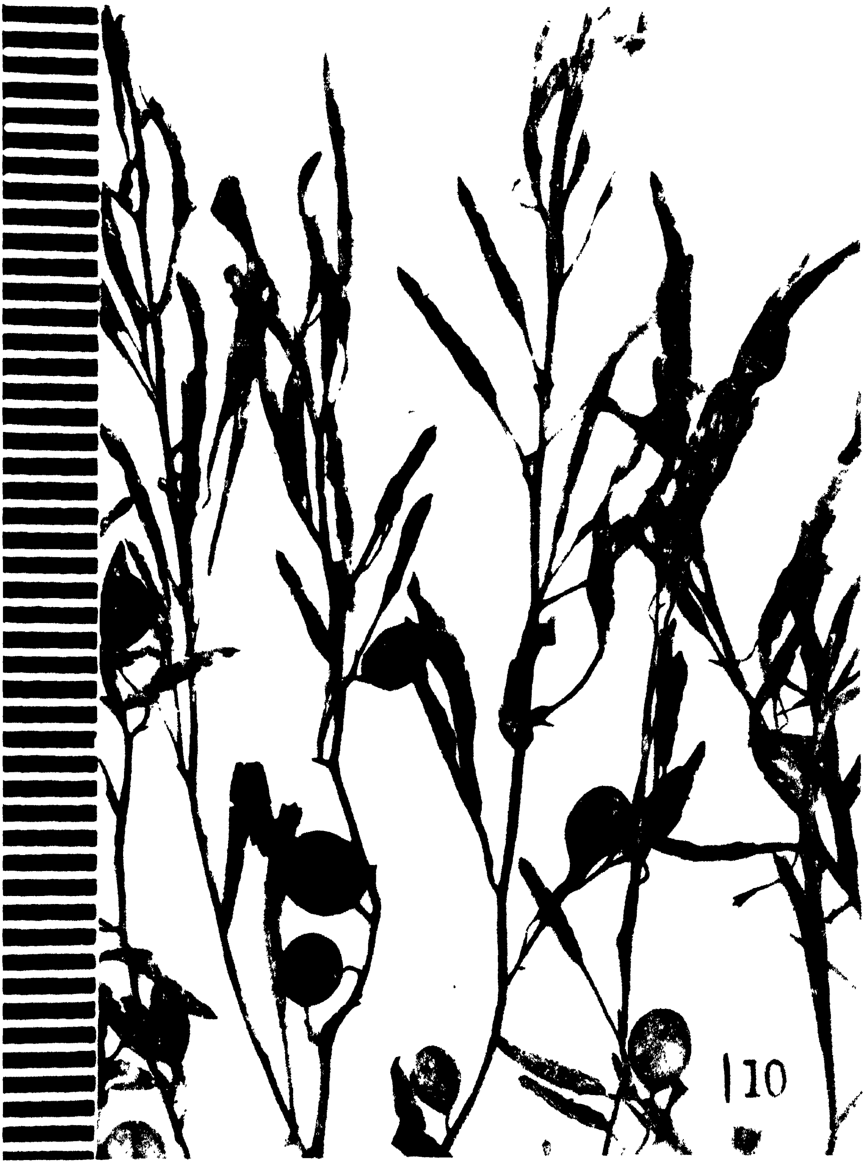
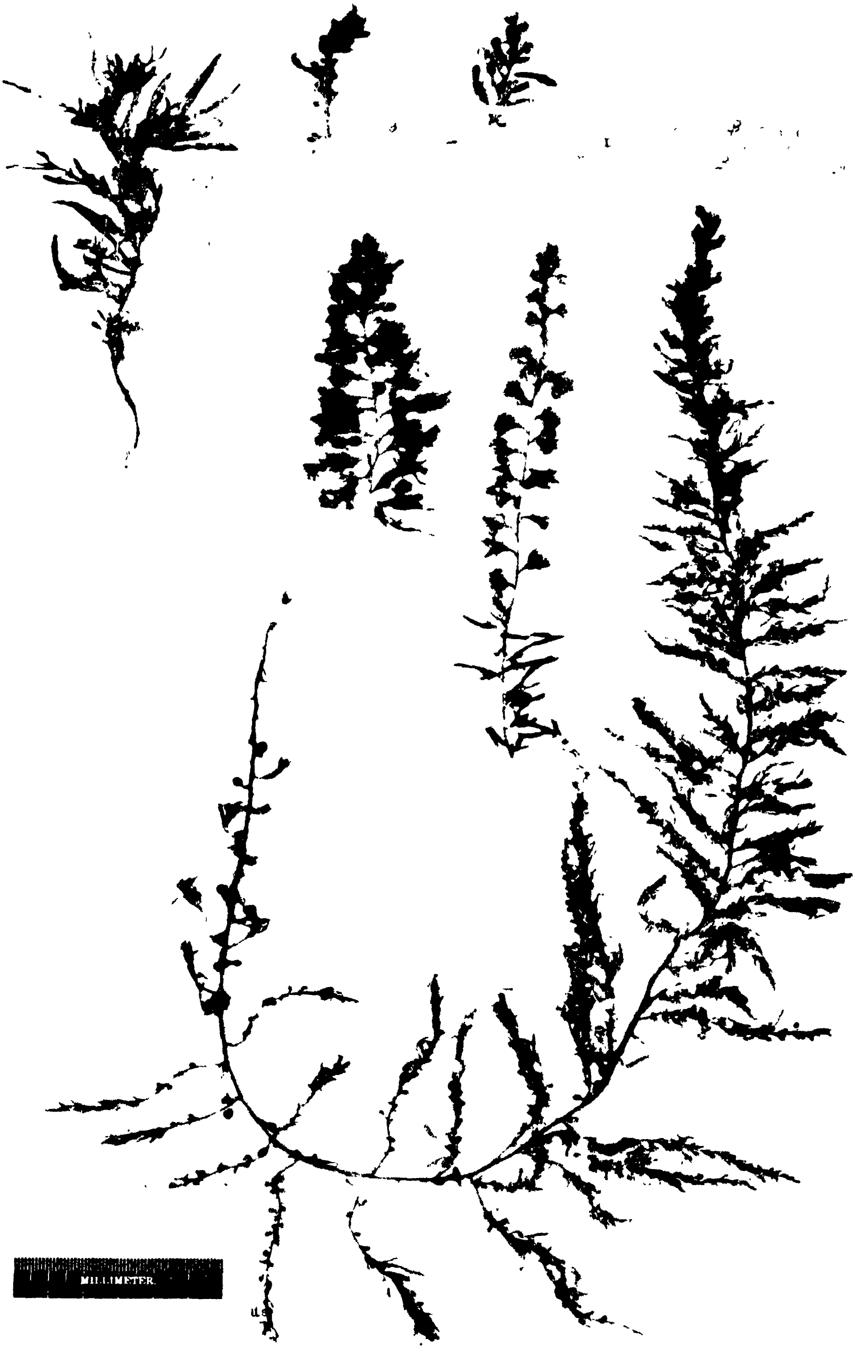

110

PLATE 45

Sargassum pallidum (Turn.) Ag.

Sheet of Turner specimens in Herb. Kew. The large specimen in the lower right-hand corner is *Fucus Acinaria* var. *pycnocistus* (Mert.) Turner.


MILLIMETER

A PRELIMINARY SURVEY OF GIGARTINA, WITH SPECIAL REFERENCE TO ITS PACIFIC NORTH AMERICAN SPECIES

BY

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BY

WILLIAM ALBERT SETCHELL AND NATHANIEL LYON GARDNER

INTRODUCTION

The genus *Gigartina* was proposed by Stackhouse in 1809, in that ill-fated paper published in the *Mémoires* of the Society of Naturalists of Moscow of which the copies were very nearly completely consumed in the burning of Moscow by Napoleon in 1812. The type species is *Fucus pistillatus* Gmelin, which appears to be the earlier *F. gigartinus* L. The generic name, as customary with Stackhouse, was taken immediately from the adjectival specific designation and is derived from the Greek word meaning "grape-stones," with the Latin adjectival ending "pertaining to" or "of collective significance." Stackhouse also, and in the same publication, created the genus *Mammillaria* to receive *Fucus mamillosus* Goodenough and Woodward, later and commonly used for a genus of Cactaceae (now a *nomen conservandum*).

In 1813, Lamouroux, apparently independently and presumably without knowledge of Stackhouse's genus, also proposed a genus *Gigartina.* Lamouroux's genus is comparatively large and composite, but in it, among other and almost entirely unrelated species, he placed the *Fucus pistillatus* Gmel. This species and *Gigartina acicularis* (Wulf.) Lamour. are the only species among the 30 referred by Lamouroux to his *Gigartina,* which may now be considered properly to belong to the genus *Gigartina* of Stackhouse.

The species of the genus, as now regarded, have passed successively through the genera *Ceramium* (Roth, 1807), *Sphaerococcus* (C. A. Agardh, 1820), to *Gigartina* (Stackhouse, 1809, Lamouroux, 1813, and Greville, 1830). Kuetzing, in his Phycologia Generalis (1843), divided them among *Gigartina* (*G. acicularis* (Wulf.) Lamour., etc.), *Chondroclonium* (*G. pistillata* (Gmel.) Stackh.), *Chondracanthus* (*G. Chamissoi* (Mert.) Mont.), *Chondrodictyon* (*G. radula,* tetrasporic type), and *Mastocarpus* (*G. mamillosa* (Good. et Woodw.) J. Ag., etc.). J. G. Agardh refounded *Gigartina* and extended its boundaries in 1842 (Alg. Mar. Medit., 103); in 1851 (Spec. Alg., 2:260) he assigned 23 species to it; in 1876 (Spec. Alg., 3:189–204) he increased these to 39 species; and in 1899 (Anal. Alg., Cont. V) he made his final revision, division into tribes, etc., and brought the number of species up to 69.

On the assumption that the genus *Gigartina,* in the sense of J. G. Agardh, contains about 88 species—which is as close as may now be determined, approximately one-quarter of them occur on the coasts of New Zealand, one-third on the coasts of western North America, 7 species along the Atlantic and Mediterranean coasts of Europe, about 2 species on the northeastern coasts of North America, 2–3 species on the eastern coast of South America, about 6 species on the coasts of Japan, 6 species on the west coast of South America, 14 species on the extratropical coasts of Australia and Tasmania (2 only in common with those of New Zealand), and 10 species on the coasts of South Africa. The different coasts thus mentioned are supposed by J. G. Agardh to have each its own peculiar species, and this will probably be substantiated in large measure after studies with a greater abundance of material become possible.

J. G. Agardh assigned 21 species to the west coast of North America and 3 have been proposed since his last paper, making 24 in all. One of J. G. Agardh's species seems clearly not to belong to the genus, viz., *Gigartina gelatinosa* J. Ag., founded on *Gloeosiphonia californica* (Farl.) J. Ag., while *G. mollis* J. Ag. is not the *G. mollis* Harv. (*Farlowia mollis* (Harv.) Farlow and Setchell), but seems to be a minor variation of *G. leptorhynchos* J. Ag. The paper of 1899, while it tends to clarify the Californian species of *Gigartina,* at least in purifying the list of some of the names of the Cape of Good Hope species assigned to it, presents even yet many problems. It is our desire to review the Californian species, in the light of all that has been published concerning them, and to present a revision which may serve as a basis for future and more certain studies.

J. G. Agardh seems always to have regarded *Gigartina* as founded by Lamouroux, and when he limited the genus in 1842 (Alg. Maris Medit., 103) he specified that the character which separates it from the other genera similar in habit is the possession of a filamentous pericarpic layer about the compound cystocarp, while it is separated from other genera which also possess such a layer by having superficial and projecting cystocarps. In his revision of 1851 he is more explicit, especially in his discussion of the three genera *Iridaea, Chondrus,* and *Gigartina* (under *Chondrus,* Spec. Alg., 2, 1:246), where he describes the special pericarpic layer as being a *concentric reticulum.* A survey of the Californian species, however, shows that, while some species possess a very definite *"pericarpium proprium"* of concentric filaments united into a compacted reticulum, others have little trace of it, and some seem to lack a *"pericarpium proprium"* entirely. Nevertheless, in every other way, all the species seem equally qualified to be referred to *Gigartina.* It may seem best, therefore, to retain these various species within the genus, but to modify the generic diagnosis in this respect. It may also happen that when the development of the cystocarps shall have been worked out for each and every one of the species, lines of cleavage within the group may appear; but although every student of the genus from J. G. Agardh and Kuetzing down to Schmitz and Hauptfleisch has remarked on the polymorphy of its species and has considered the desirability of its division among several genera, none, other than Kuetzing, has brought forward any definite suggestions, and those of Kuetzing do not seem to obtain approval. The genera of Kuetzing may, however, if the type (or typical) species be taken as indicators, serve to segregate the group of gigartinoid forms and, the various subdivisions, tribes, etc., of J. G. Agardh's various accounts being taken into consideration, be used as subgenera until some more satisfactory solution of the problem may be found. Such subdivision into subgenera must seek to segregate the 75 species (more or less) into groups having, in common, and distinctive of one or another group within the assemblage, characters of habit, structure, and peculiarities in cystocarpic and tetrasporic structures. After studying, so far as present opportunities allow, the entire content of species attributed, at present, to the genus, it seems best to consider them under the present generic name *Gigartina,* as established by Stackhouse in 1809, and to suggest the following tentative arrangement, emphasis being laid upon the Californian species so far as they may be representative.

Gigartina Stackh. (*lim. mut.*). Members of the *Gigartineae* with hemispherical or spherical, protuberant cystocarps.

Series A. Fronds terete to complanate; lateral branches numerous, pinnate to subpinnate; cystocarpic spore mass with a looser or denser, proper (i.e., differentiated) pericarp........*Pinnatae*

1. *Eogigartina* (*Aciculares* J. Ag., p.p.). Fronds terete to somewhat flattened, lateral branching subquadrifarious; cystocarps not in fixed position. Typical species *G. acicularis* (Wulf.) Lamour.

2. *Mesogigartina.* Fronds terete to slightly compressed, lateral branching quadrifarious; cystocarps borne seriately in short differentiated branchlets. Typical species........*G. serrata* Gardner

3. *Eugigartina* (*Gigartina* Stackh.). Fronds compressed to flattened, not strictly complanate; lateral branches distichous (all marginal); cystocarps scattered or grouped on the short lateral branchlets. Typical species *G. pistillata* (Gmel.) Stackh.

4. *Chondracanthus* (Kuetz., as genus; *Chondroclonium* Kuetz.). Fronds complanate; lateral branches regularly marginal, short proliferous branchlets from flat surfaces; cystocarps and tetrasporic sori on short leaflets or papilloid branchlets, marginal or superficial. Typical species........*G. Chauvinii* (Bory) J. Ag.

Series B. Fronds with longer or shorter cylindrical stipes, slightly dichotomous or, at times, pinnately branched, expanding above into large, flat blades, the latter in turn sparingly split or proliferous from the margins or the surfaces; cystocarps protruding entirely, sessile or on short stalks, single or clustered; spore mass of the cystocarps with a dense proper pericarp........*Magnifoliatae*

5. *Cheilogigartina* (*Radulae* J. Ag., p.p.). Terminal fronds with intramarginal zone naked (i.e., destitute of papilloid outgrowths), papilloid outgrowths usually crowded; tetrasporangial sori in verrucae or papillae (projecting from surfaces and margins). Typical species *G. californica* J. Ag.
6. *Chondrodictyon* (Kuetz., as genus). Terminal fronds with intramarginal naked zones, papilloid growths crowded or, often, distant from one another, on both surfaces and margins; tetrasporangial sori immersed in the blades, adjacent to one or the other surface but not projecting. Typical species *G. bracteata* (Gmel.) comb. nov. (*Chondrodictyon capensis* Kuetz.) and *G. volans* (Ag.) J. Ag.

Series C. Fronds complanate, at least above, dichotomous or palmately branched; lateral branches as irregular proliferations, marginal or superficial; cystocarps protruding, sessile or pedicellate; cystocarpic spore mass lacking a proper pericarp........*Palmatae*

7. *Mastocarpus* (Kuetz., as genus, *lim. mut.*; *Mamillosae* J. Ag.; *Mammillaria* Stackhouse). Fronds with margins slightly to decidedly revolute and usually lacking papilloid outgrowths; cystocarps single, glomerate, or seriate on specialized, short, superficial pinnules (papilloid). Typical species *G. mamillosa* (Good. et Woodw.) J. Ag.

The main features of the arrangement presented earlier, to serve as a guide in the attempt to subdivide the genus *Gigartina* (*in sensu amplissimo*) into practicable units and seemingly reasonable groups of cleavage, indicate that the chief reliance has been placed on variance as well as resemblances in branching, on concomitant characters, particularly of details of microscopic structure of the frond (not mentioned in the survey above), and on the differentiation of the tissues in the region of the cystocarp. When J. G. Agardh (Alg. Mar. Medit. et Adriat., 1842, 103) "reformed" the genus *Gigartina* of "Lamouroux" he stressed the reticulate filamentous structure of the interior of the frond, the densely crowded moniliform threads (anticlinal) in the cortex, and the differentiation of a filamentous pericarp layer, or proper pericarp, within the outer tissues and surrounding the *"favellidia"* of conglobated spores. Later on, this *pericarpium proprium* was described (J. G. Agardh, Spec. Alg., 1, 1:246–261, 1851) as within the outer pericarp, and as made up of a reticulate tissue of ambient concentric filaments. By this character *Gigartina* is to be distinguished from *Chondrus*, while from *Iridaea* and *Rhodoglossom* it is to be distinguished by its definitely emergent cystocarps. In his 1842 paper, J. G. Agardh included not only the two Mediterranean species, viz., *Gigartina Teedii* (Roth) Ag. and *G. acicularis* (Wulf.) Lamour., but also mentioned others, including *G. mamillosa* (Good. et Woodw.) J. Ag., which have no proper pericarp. However, the last does have projecting cystocarps. This species was the first mentioned by Kuetzing (Phyc. Gen., 398) in proposing his genus *Mastocarpus*, and he delineates the cystocarp (*loc. cit.*, pl. 76, III) without any proper pericarp. Consequently, if we are to retain *Gigartina* in the larger sense, the distinguishing character of the possession of a *peri-*

carpium proprium must be omitted from the diagnosis, but should we separate *Gigartina mamillosa* and its group of closely related microspecies under *Mastocarpus* Kuetzing (*lim. mut.*), this inconsistency is avoided. The remaining groups, however, are not all in perfect agreement with the requirement of a medullary reticulum of filaments in the frond. *Gigartina serrata* Gardner, for example, seems to have the main frond more or less parenchymatous, at least such is the appearance in cross-section. Some other species show something similar, but the outer tissues and the branchlets show the filar reticulum postulated for members of the genus. Were the details of structure definitely determined for all the species and for different portions of each plant and in different stages, it might possibly happen that lines of cleavage or adherence might be found. Such investigation must await leisure and opportunity.

The division of the broader *Gigartina* into three series is largely upon the branching of the frond. It may be that here is a suggestion of generic cleavage. Series C (*Palmatae*) has certain other characters than the dichotomous or palmate branching, not seriously complicated by frequent proliferation which is largely from the surfaces. In the *Palmatae* the margins of the frond tend to recurve (or incurve), giving the narrower forms a decidedly canaliculate appearance. The margins also are generally free from the fertile papillae. The spore mass lacks a proper (or inner) pericarp. For this group it may be desirable to revive the generic name *Mastocarpus* of Kuetzing (Phyc. Gen., 298, 1843), excluding, however, all the species referred to it except *M. mamillosus* (*M. papillatus* of Kuetzing being not the *Sphaerococcus papillatus* Ag. but the *Gigartina Kuetzingii* nom. nov., a very different type). Question also may be made of *Mammillaria* Stackhouse (Tentamen, 1809, p. 55), now a *nomen conservandum* for a cactaceous genus.

Series B (*Magnifoliatae*) has distinct and usually readily recognizable life forms (or habit). The stipes are abbreviated, sometimes branching once or even twice, dichotomously, and then expanding into long, narrower or broader laminae, which show little further division, furcate at times, but also at times with small marginal proliferations. They seldom show anything of regular pinnation. The margins are usually coarsely or finely dentate and both the margins and the surfaces are covered, now sparsely, now profusely, with papilloid fertile projections, but leaving a more or less conspicuous intramarginal zone, temporarily or permanently free from them. Series B therefore seems to be well separated from the other two series and might be segregated as a distinct genus were it not for the fact that its species seem to separate again into two distinct groups, the one we have designated as *Cheilogigartina* having the tetrasporangial sori confined to verrucose or papilloid emergences, the other, the genus *Chondrodictyon* of Kuetzing, having the tetrasporangial sori immersed in the cortical layers of the blades. The type species, *Chondrodictyon capense* Kuetzing (Phyc. Gen., 396, 1843, and Tab. Phyc., 17:6, pl. 21, 1867), is not the *Fucus radula* Esper (Icon. Fucorum, 5:3, pl. 113, 1802), as has been assumed by J. G. Agardh and others, but is properly *Gigartina bracteata* (Gmel.) Setch. et Gard. The only Californian species to be assigned to *Chondrodictyon* are *Gigartina volans* (Ag.) J. Ag., and *G. velifera* J. Ag.

While Series B seems fairly homogeneous and well set off from the others and Series C also shows itself fairly well separated but divisible into two subgroups, Series A, the *Pinnatae,* while containing within itself a certain coherence as to developmental sequence, yet segregates into at least four subgroups, represented respectively by *G. acicularis, G. serrata, G. pistillata,* and *G. Chauvinii.* The first subgroup is more or less quadrifarious in the branching of the terete or only slightly compressed fronds, and has no specialized fruiting branchlets. *Gigartina acicularis* (Wulf.) Lamour. may possibly represent a very simple, even primitive, type of the *Gigartina* series. The approach to a cylindrical frond, with at least some tendency to dichotomy (or often rather subdichotomy) and no specialization of fertile branchlets, coupled with a somewhat projecting cystocarp of the Gigartinaceous type (with *pericarpium proprium aut internum* distinctly differentiated), causes it to stand out for inclusion in an *Eogigartina* subgenus (or even genus?). There may be added to *G. acicularis* at least *G. Chapmannii* Hook. f. et Harv. and *G. Kroneana* Rabenh. (see Laing and Gourlay, Trans. N. Z. Inst., 60:109–112, 1928), as well as *G. divaricata* Hook. f. et Harv. (see Laing and Gourlay, *loc. cit.,* p. 106) of the New Zealand species, *G. glomerata* M. A. Howe (Mar. Alg. Peru, 103, pl. 39, pl. 40, figs. 1–11, 1914), and *G. tuberculosa* (Hook. f. et Harv.) Grun. of Peru (see Howe, *loc. cit.,* 105, pl. 40, figs. 12–17, pl. 41), and the latter also from the Chatham Islands of New Zealand (see Laing and Gourlay, *loc. cit.,* 133 and fig. 26). *Gigartina fastigiata* J. Ag. of South Africa seems also to belong to this group, as do also *G. tenella* Harv. and *G. intermedia* Suringar of Japan. The members of the subgenus *Eogigartina,* whose branching is fundamentally more or less dichotomous, with the lateral branching multifarious or perhaps more properly subquadrifarious (see Laing and Gourlay, Trans. N. Z. Inst., *loc. cit.,* p. 104) suggest a simpler or more primitive condition of the *Gigartina* complex, as mentioned previously, and as is indicated by the prefix of the subgeneric name, *Eogigartina.* The branching in all the *Gigartina* species is primarily dichotomous. This is to be seen regularly developed throughout in some species, but may be only expressed in the earlier one or two divisions of the frond, and, in many, one fork of the presumable dichotomy overtops the other and a subdichotomous main branching is produced. Lateral branchlets, however, are more or less abundant according to the group and according to the species. In *Eogigartina,* these lateral branchlets are described as multifarious, but early in our own studies the suggestion of quadrifarious or subquadrifarious came to us, and Laing and Gourlay (*loc. cit.*), from the abundant and varied living material of their New Zealand species, have verified it, quoting Harvey (Crypt. Bot. Antarct. Voy., 76, 1845). In *Eogigartina,* as might be expected, the lateral branchlets are nonspecialized or little specialized, as bearers of the reproductive bodies. In *Mesogigartina,* specialization, as earlier indicated, is definite, but the short, more or less uniform lateral fertile branchlets are subquadrifarious. In both the subgenera just mentioned the frond is cylindrical to slightly compressed.

In *Eugigartina,* or *Pistillatae,* compression and some specialization of lateral fertile branches together modify a normally dichotomous or subdichotomous frond into one which is dichotomously compound pinnate, little or no evidence of tetrastichous arrangement remaining. In *Chondracanthus,* however, the greater degree of flattening to a comparatively thin complanate frond, dichotomous or subdichotomous chiefly at the base, and pinnate in the main branching above, results from the quadrifarious (or tetrastichous) arrangement of the lateral branches. From the margins of the principal elongated and complanate divisions, long, complanate, generally compound (or decompound) lateral branches emerge, while, from the surfaces, a single longitudinal series of short fertile branches appears in the narrower portions, but becomes multiseriate on the broader divisions until the surfaces of the frond may be covered with them, more sparse or more crowded, according to the species. There may remain, however, an intramarginal zone (on each side of each surface, naked, or free from these short modified fertile branchlets). The existence of this zone seems consistent with the hypothesis of development from a tetrastichous arrangement of lateral branches or branchlets.

As the surface area of the terminal blade increases, as happens in the species of the subgenera *Cheilogigartina* and *Chondrodictyon,* the existence of these naked intramarginal zones seems, from what has gone before, to indicate the persistence of the primitive influence of tetrastichy of the lateral structures throughout the six subgenera mentioned and to hypothesize the existence of zygomorphic (possibly dorsiventral) rather than radial symmetry even in those simpler species of *Gigartina* where the frond is terete. The progression from *Eogigartina* through *Mesogigartina, Eugigartina,* and *Chondracanthus* to *Cheilogigartina* and *Chondrodictyon* seems normal and to afford legitimate argument for retaining these six groups as subgenera of one large polymorphic genus.

While the six subgenera just considered seem to form a progressive sequence from such a primitive type as that of *Gigartina acicularis* (*Eogigartina*) up to such modified types as those of *G. californica* (*Cheilogigartina*) and *G. volans* (*Chondrodictyon*), the species grouped under Series C seem reasonably homogeneous, but to depart very considerably from the lines represented by Series A and Series B. The derivation of the species of *Eogigartina* from a simple *Chondrus* type does not seem to be immediate. In the first place, the tetrastichous tendency is only obscurely, if at all, represented in *Chondrus,* and, in the second place, *Chondrus,* as typically represented by *C. crispus* (L.) Stackh., has no *pericarpium proprium.* Series C, however, as we have outlined it for *Gigartina,* does have both of these typically *Chondrus* negative characteristics, viz., no strict *tetrastichy* and no *pericarpium.* The more simple, undifferentiated species, such as *Gigartina unalaschcensis* (Rupr.) Rupr., resemble certain forms of *Chondrus crispus* so closely, in certain states at least, as to be segregated with difficulty. *Chondrus crispus,* however, as may be seen from the illustrations (see Turner, Fuci, pls. 216, 217, 1819; Harvey, Phyc. Brit., 1: pl. 63, 1846; Kuetzing, Tab. Phyc., 17, pls. 49, 50, 1867; and above all Lamouroux, Diss., pls. 1–18, 1805) of the various types of plants assigned to it (some of which, however, are Gigartinas of the Series B), shows a polymorphism extending to close resemblances to *Gigartinae* of Series C. If for the plants of Series C we choose to resurrect the name *Mastocarpus* of Kuetzing (as genus? or as subgenus?), limiting it to the *Mastocarpus mamillosus* (Good. et Woodw.) Kuetz. as type, we shall then obtain a series of plants ranging from the simplest Chondroid forms, such as *G. unalaschcensis,* through the microspecies of J. G. Agardh and others, *G. sitchensis* (Rupr.) Rupr., *G. mamillosa* (Good. et Woodw.) J. Ag. (or *G. stellata* (Stackh.) Batters) and some of its forms not yet raised to microspecific rank, through *G. papillata* (Ag.) J. Ag. (as to the Californian plant), *G. Agardhii* Setch. et Gard., to *G. Jardinii* J. Ag., as representing a series in which the divisions of the dichotomous frond constantly become narrower and more completely and characteristically canaliculate. Finally we may consider, with propriety, the possible inclusion of such austral species as *G. alveata* (Turn.) J. Ag. and *G. ancistroclada* Mont. of New Zealand and Tasmania, respectively, with a possibility of considering also as extremes *G. tuberculosa* (Hook. f. et Harv.) Grun., *G. angulata* J. Ag., and *G. insidiosa* J. Ag. The distinctive feature, other than the protuberant to pedicellate cystocarps, the lack of a *pericarpium proprium,* and the palmately, dichotomous, more or less canaliculate frond, is the character of the margins. These are prominent, as compared with others of the *Gigartina* assemblage, because of their rounded and incurved (or recurved) character and are made more conspicuous by their almost entire lack of emergences, being almost always entirely naked. When the divisions of the frond become very broad, as in *G. latissima* (Harv.) Eaton, the curling of the margin relative to the flatness of the blade becomes so slight as to disappear, but its nakedness remains. On the other hand, as the divisions of the frond become very narrow, the curling becomes proportionally so great as to result in narrow, channeled segments of the frond, from just above the base to the very tip. Certain species of *Chondrus,* particularly *C. canaliculatus* (Ag.) Grev. and *C. affinis* Harv., show channeled fronds, but the former, at least, has something of a "well developed" *pericarpium proprium* (see M. A. Howe, Mar. Alg. Peru, 99, 106, 1914).

The cystocarps in Series C are on emergences, from pustular to cylindrical, straight or curved, simple or branched, borne singly or bunched together, or even serrate on the longer superficial branchlets. There is one species, *Gigartina pacifica* Kjellman (Kongl. Svenska Vetensk.-Akad. Handl., 23, 8 :31, pl. 1, figs. 21, 22, 1889, excl. syn.), belonging to the *Mastocarpus* series on account of its curled margins, which departs from the type as outlined above, in that it has papillate fertile branches at the apices and on the margins, as well as on the surfaces, of the divisions of the frond. It is probably close to *Chondrus mamillosus* var. *ochotensis* of Ruprecht (Tange Och. Meer., 318, 1851) but probably does not include Ruprecht's other two varieties, *unalaschensis* and *sitchensis* (Ruprecht, *loc. cit.*). *G. pacifica,* as limited by Kjellman's description and illustration, seems probably confined to the Ochotsk Sea and the northern shores of Japan (see also Yendo, Bot. Mag. Tokyo, 30 :54–59, figs. 2–4, 1916, where fig. 2 and fig. 4 are certainly of *G. pacifica* Kjellm.). The strictly marginal outgrowths of *G. pacifica,* occasional in *Chondrus crispus* and very rare in microspecies of Series C other than *G. pacifica,* present no difficulties in assumed phylesis, but make modification of general diagnosis less certain. The general characteristic of *Mastocarpus* (genus or subgenus, as limited from Kuetzing's conception) depends, then, upon the curled or involute margins of the segments of the frond. In the *Eumamillosae* these margins are seldom proliferous, in the *Pacificae* they are normally proliferous, while in the *Alveatae* the margins are normally bare and the tips are downwardly curved or curled. In the *Alveatae* the cystocarps are all practically sessile or, at most, very short pedicellate. In all the sections, the cystocarps are devoid of an inner pericarpic layer and no tetrasporangia have, as yet, been detected.

The species of Gigartina of the west coast of North America have been variously referred by different writers, but we may take J. G. Agardh's account of 1899, previously quoted, as the basis for the brief survey here included. In all, about 24 species have been enumerated. In

1903, one of the writers (W. A. S.) visited Lund and was allowed to study the Agardhian types, and recently Professor Harald Kylin has most kindly caused photographs of the type specimens to be made and forwarded to us. With this assistance, the following account has been prepared.

SERIES A. PINNATAE

The four subgenera segregated from one another, but united under this series, show progressively the advance from the simplest type (*Eogigartina*) through intermediate types (*Mesogigartina* and *Eugigartina*) to the ultimate development of the true Pinnatae in *Chondracanthus*. The feature in common is the arrangement and representation of the tetrastichous, or by reduction (?) distichous, lateral branches.

Subgenus 1. EOGIGARTINA

No species of this subgenus has as yet been detected on, or referred to, the west coast of North America.

Subgenus 2. MESOGIGARTINA

1. **Gigartina serrata** Gardner

Gardner, Univ. Calif. Publ. Bot., 13:334, pls. 60–62, 1927.

The species is well illustrated by Gardner and seemed at first to be closely related to *Gigartina Lessonii* (Bory) J. Ag. as illustrated and distributed by M. A. Howe (Mar. Alg. Peru, p. 100, pl. 37, 1914), who has apparently compared his specimens with the types. *Gigartina serrata,* however, is a coarser, more rigid plant, with the fertile branchlets subquadrifarious extending outward and upward and neither distichous nor with the drooping curvature of those of *G. Lessonii.* The main branches are in a single plane, dichotomous or subdichotomous, and appear to be distichously pinnate but irregularly so. The fertile branchlets are short and tetrastichous. It probably includes *G. canaliculata forma laxa* Collins (Phyc. Bor.-Am., 23: no. 1139, 1903), distributed without diagnosis and (in our copy) not well developed.

Gigartina serrata Gardner has been found at Balboa and San Diego in southern California and at Ensenada, Mexico (type locality).

Subgenus 3. EUGIGARTINA

2. **Gigartina canaliculata** Harv.

Harvey, *in* Hooker and Arnott, Bot. Beech. Voy., 490, 1841; Ner. Bor.-Am., 2:174, pl. 27, *C,* 1853.

The species is narrow, decidedly compressed, dichotomous or subdichotomous below to regularly distichously pinnate above. The fertile ramuli are short, also distichously pinnate, terminating, as to the branches and branchlets, in sharp aculeae. The cystocarps are borne singly or crowded on the fertile ramuli, blunt or with one or more subapical aculeae. The plant is well illustrated by Harvey (Ner. Bor.-Am., 2: pl. 26, *C*, 1853) and by Kuetzing (Tab. Phyc., 17: pl. 69*c–e*, 1867), except that they emphasize the "canaliculate" character seen only in dried plants or in those incompletely swollen after being dried. The fresh plants have the surfaces plane to rounded outward. The ascription of this canaliculate character to this species, both as to specific name and as to diagnostic character, has obscured the reasons for its placing in the genus, such as associating it with *G. alveata, G. ancistroclada,* and *G. tuberculosa,* with which it has no real affinity. The fairly regularly pinnately decompound upper portions of the frond and the short fertile branchlets, together with narrow, compressed rather than complanate frond, place it near to *Gigartina pistillata,* from which it differs in the bristly appearance due to the numerous aculeate tips of branches, branchlets, and ramuli. In this respect *G. canaliculata* suggests *G. Teedii,* but *G. Teedii* is a more complanate species (i.e., thinner, relative to its breadth) and, in its broader forms, shows a tendency toward tetrastichous ramuli, while *G. canaliculata* seems strictly distichous.

Gigartina canaliculata Harv. extends from the central coast of California down to the central Pacific coast of Lower California (California Baja) in Mexico.

Subgenus 4. CHONDRACANTHUS Kuetz.

Kuetzing, Phyc. Gen., 399, 1843, as *genus proprium; Chondroclonium* Kuetz., Phyc. Germ., 302, 1845.

Kuetzing changed his *Chondracanthus* to *Chondroclonium* on account of the previous use of the former name for a genus of worms. In 1843, he assigned to it *Ch. Chamissoi* (Mert.) Kuetz., which he illustrated on plate 75, II, *Ch. Teedii* (Roth) Lamour., and *Ch. Chauvinii* (Bory) J. Ag., all fairly thin complanate species with slight dichotomy below, decompoundly pinnate above, with fertile ramuli, short, distichous along the margins, and tetrastichous (from the surfaces) in the broader specimens, the Kuetzing inclusion verging toward *Eugigartina* except that *Gigartina Chauvinii* (Bory) J. Ag. departs toward the broader tetrastichoid types added later by J. G. Agardh.

The species, besides the western North American, may be thought of as including at least *Gigartina Chamissoi* (Mert.) J. Ag. (w. S. Am.), *G. Teedii* (Roth) Lamour. (Eur.), *G. elegans* Grev. (Brazil), *G. Chauvinii* (Bory) J. Ag. (w. S. Am.), *G. stiriata* (Turn.) J. Ag. (S. Africa), *G. angulata* J. Ag. (N. Z.) and possibly even the very broad *G. atropurpurea* J. Ag. (N. Z.). These are all pinnated forms with scant to abundant superficial as well as marginal fertile branchlets (i.e., pinnately tetrastichoid).

3. Gigartina Chauvinii (Bory) J. Ag.

J. G. Agardh, Alg. Mar. Medit., 104, 1842; *Sphaerococcus Chauvinii* Bory *in* Duperry, Voy. Coq., *5*, 2, 1: 165, 1829, and pl. 20, fig. 1, 1826.

Sphaerococcus Chauvinii was segregated by Bory (*loc. cit.*) into three groups, var. *α latissimus,* having fronds broad, exasperate-confused, and with pinnules long, lanceolate furcate. Here he refers to the plant indicated as no. 1 of his plate 20, and this may be taken as the type of his species. The borders of the pinnules are obliquely lacerate, the substance seems thinner, and the color is more greenish purple. It seems to be the plant collected on the coast of Peru by Coker, and described, figured, and distributed by M. A. Howe under *Gigartina Chauvinii* (see M. A. Howe, Mar. Alg. Peru, 101, pl. 38, 1914). The cystocarps of this form are probably those represented in figure 4 of Bory's plate 20, and, as seen in Howe's and other Peruvian specimens, are sessile and numerous on the foliaceous fertile pinnules of var. *α*. Bory's var. *β intermedius* has the frond narrow, ornately pinnatifid, with the pinnules very long, lanceolate, and not bifid. This is represented by figure 2 of Bory's plate 20, which seems a distinct microspecies, at least the pinnules are neither so foliaceous nor so obliquely laciniate as in var. *α*. This form of Bory is represented as being dark red. The cystocarps are large, single, with a slender, straight, cylindrical pedicel, not borne on laciniate flattened leaflets as in var. *α*. A form close to var. *β* has been found on the Californian coast and is described farther on as *Gigartina Boryi* Setchell and Gardner.

The third form of Bory, var. *γ angustus,* has the fronds linear, narrow, with the pinnules ciliate, and very flaccid. Bory figures a fragment of this under no. 3 of plate 20. It seems to have something of the habit of *Grateloupia filicina.* No fruit is indicated, and the original specimen may confirm a suspicion that it may be antheridial.

Setchell and Gardner (Proc. Calif. Acad. Sci., ser. 4, 12:744, pl. 46*b*, pl. 70, 1924) referred specimens from two islands in the Gulf of California to *Gigartina Chauvinii.* The narrow plant (*loc. cit.,* pl. 46*b*) closely resembles some of the Peruvian specimens distributed by M. A. Howe. The broader plants (pl. 70), while resembling closely Bory's figure 1 of his plate 20, do not exactly correspond and it may be that this form, concerning which doubt was expressed at the time of publication, may come nearer to J. G. Agardh's *G. Farlowiana,* of which more will be said later, but it seems to be a narrower plant as well as thinner and more membranaceous. Its color is red, not greenish, as described by both Bory and M. A. Howe. It will be left, for the present at least, under *G. Chauvinii,* although its general habit of being broader than high may characterize it as a variety, if not as a distinct microspecies. It has occurred to us only in the islands in the Gulf of California.

4. **Gigartina leptorhynchos** J. Ag.

Plate 46

J. G. Agardh, Till Alg. Syst., VII:28, 1885; Anal. Alg., Cont. V:13, 1899. *Gigartina microphylla* var. *horrida* Farlow, Proc. Am. Acad., 10:370, 1875; Farlow, Anderson, and Eaton, Alg. Exs. Am. Bor., no. 79, 1878; *Gigartina horrida* Farlow, *in* C. L. Anderson, Zoe, 2:3, 1891; Collins, Holden, and Setchell, Phyc. Bor.-Am., 3: no. 137, 1895. *Gigartina mollis* J. G. Agardh, Anal. Alg., Cont. V:13, 1899 (non *G. mollis* Harv. et Bail., which is *Farlowia mollis* (Harv. et Bail.) Farlow and Setchell, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., 18: no. 898, 1901).

Gigartina leptorhynchos is even more narrow than *G. Chauvinii.* When young, the flattening of the narrow irregularly pinnate frond may be seen, but this is soon covered by bristly, short, cylindrical pinnae, and the frond itself thickens to compressed or almost cylindrical. The extreme bristly appearance of the adult plant well deserved the name "*horrida*" given to it by Farlow, but, as J. G. Agardh remarks (Till Alg. Syst., VII:28, 1885), the species is much more closely related to *G. Chauvinii* than to *G. microphylla* (*G. Harveyana*). Although bristly in appearance and rough when dried, when fresh or soaked out from the dried state it is pleasantly soft and might merit the term "*mollis.*" The name "*leptorhynchos*" may have been applied by J. G. Agardh to indicate the slender, delicate "bristles" which are so characteristic of the species. Plate 46, from specimens in Herb. J. G. Agardh, at Lund, shows a variety of small plants of different ages. Fairly broad and otherwise luxuriant plants occur, which are probably the *G. mollis* of J. G. Agardh (not of Harv. et Bail.), since these show an approach toward *G. Chauvinii.* Their bristly character, however, distinguishes them.

The species is distributed from about Monterey and Pacific Grove southward to Ensenada, Mexico, and probably even farther south.

5. **Gigartina echinata** Gardner

Gardner, Univ. Calif. Publ. Bot., 13:335, pls. 63, 64, 1927.

The species is narrow, flat, more so in the tetrasporangial plant than in the cystocarpic, dichotomous or subdichotomous for one or two divisions, above pinnately decompound with acute angles and rigid, divaricate, sharply aculeate branchlets in tetrastichous arrangement. The tetrasporangial sori and cystocarps are sessile on the sides of short pinnules from both margins and surfaces, overtopped by one or coronate with several aculeate tips. Thus far, *Gigartina echinata* is known, with certainty, only from the coasts of southern California, with the type locality at Avalon on Santa Catalina Island. It has also been found at La Jolla and is doubtfully reported, possibly as drift, from Santa Cruz on the middle Californian coast.

The plants of *Gigartina echinata* are distinct in their general aspects from any referred to *G. Chauvinii* and are more rigid, red, paler toward the extremities, with the fertile pinnules of the margins stout, terete, and not flattened and foliaceous as in *G. Chauvinii.* They are always much more narrow than those of *G. armata* J. Ag. and others of the "broader" species of the subgenus *Chondracanthus.*

6. **Gigartina Farlowiana** J. Ag.

Plate 47, figure 1

J. G. Agardh, Anal. Alg., Cont. V:15, 1899.

The plants of the species belong to the broader series under the subgenus *Chondracanthus,* in that the rather long, stout, compressed stipe, sometimes once or twice subdichotomous, usually expands into one or more long but moderately broad blades. These, foliaceous in themselves and with a certain number of lateral expanded pinnae, have the lower pinnules at least narrowed basally into a slender, compressed (not complanate), stipe-like attachment in this and in the following species.

Plate 47, figure 1, shows the type of *Gigartina Farlowiana* in Herb. J. G. Agardh at the University of Lund. The type specimen, as may be seen from the figure, represents only the terminal portion of an apical broad blade with laciniately crisped marginal projections, and surface papillae which are prolonged (or decurrent) downward. The pinnae from the margins of the main blade are contracted at their bases and somewhat thickened at that point, but both characters are less pronounced than in the next species. The pinnae, also, emerge at a very acute angle and point upward, while those of the following species are decidedly patent. Fertile pinnules both of margins and of surfaces are more compressed than cylindrical and both sori and cystocarps are irregularly grouped.

Gigartina Farlowiana J. Ag. is middle to southern in its distribution, extending from the Monterey Bay region to La Jolla in the San Diego region.

7. **Gigartina Boryi** sp. nov.

Plates 48 and 49

G. fronde e disco orienda, deorsum longe stipitata, supra longe et gradatim dilatata, moderate subdichotoma, in laminam longam angustamque regulariter et frequenter pinnatam, usque ad 55 cm. longam et 3 cm. latam expansa; pinnis numerosis, confertis, dimorphis, pinnis longioribus oblanceolatis, foliaceis, basi in stipite compressa, anguste contractis, marginibus serratis aut pinnulis fertilibus curtis ornatis, pinnis curtioribus cylindricis aut apice leviter dilattais; soris tetrasporangialibus et cystocarpiis in pinnulis marginalibus aut superficialibus lateraliter positis, cystocarpiis pedicellis gracilibus curtisque, marginalibus regulariter seriatis in pinnis, tetrasoris superficialibus, in pedicellis curtis crassioribusque sparsis; zonis intramarginalibus nudis.

Specimen typicum cystocarpicum Herb. Univ. Calif., no. 294525, tetrasporangiale Herb. Univ. Calif., no. 294522, Pacific Grove, California, legit. N. L. Gardner.

Gigartina Boryi is dedicated to the memory of Bory de Saint-Vincent, since it resembles so closely one of the plants illustrated by him in the Atlas of the Voyage Coquille, under the name of *Sphaerococcus Chauvinii* var. *β intermedius,* plate 20, that it may prove to be inseparable from it. Reasons for suspecting that Bory included two species (microspecies?) under his *Sph. Chauvinii* have been given earlier in this account. The Californian plant described here seems to have the pinnae more strikingly regular and numerous and possibly given off at a somewhat broader angle than in the Peruvian plant. The fertile pinnules cover both margins and surface of the main frond and of the pinnae, leaving a more or less intramarginal zone on each surface free from them. This last feature is usually more readily noticed in younger plants. The plants have an entirely different aspect from any other Gigartinas from the west coast of North America.

While the Monterey Bay region (Pacific Grove) is the type region, plants seeming to belong to this species have been received also from the San Diego region (La Jolla).

8. **Gigartina armata** J. Ag.

Plate 47, figure 2

J. G. Agardh, Anal. Alg., Cont. V:15, 1899; De Toni, Syll. Alg., 4, 5:180, 1924.

J. G. Agardh describes this species as having a frond membranaceous rather than coriaceous and tending toward red rather than purple in color. The ramification is decomposite pinnate, with the new lanceolate pinnae arising repeatedly along the margins. The type has the adult leaf lanceolate and about 5 cm. broad at the middle portion, while the younger leaves are rather linear. The margins are never thickened, but often excurrent into small pinnules and into cystocarps smaller than those of *G. spinosa* Kuetz. Under *G. asperifolia* (*loc. cit.,* p. 16) he speaks of *G. armata* as having a decompositely pinnate frond as compared with the laciniate frond with few bifurcations of *G. asperifolia,* which resembles more nearly the simple frond of *G. Harveyana.* He also speaks of the "asperities" of the frond of *G. asperifolia* being more like those of *G. armata* and unlike those of *G. Harveyana.* What may be taken as the type specimen (see pl. 47, fig. 2) under no. 23714 Herb. J. G. Agardh at Lund, is a specimen distributed under no. 124 of Farlow, Anderson, and Eaton, Algae Exsiccatae Americae borealis, from San Diego, California, collected by Dr. E. Palmer. Unfortunately the distribution is not uniform, the copy at the University of California containing three specimens of very different aspect, only one of which seems likely to be referred to this species. The pinnae are somewhat contracted at the base, but are nevertheless broad and, except for the lowest, are not thickened or stipe-like. The margins above are beset with flat laciniate pinnules, while on the surface the pinnules are reduced to short tetrasporangial or cystocarpic papillae. The distribution covers the San Diego region, extending to Ensenada, Mexico.

9. Gigartina asperifolia J. Ag.

Plate 50

J. G. Agardh, Anal. Alg., Cont. V:15, 1899; De Toni, Syll. Alg., 4, 5:180, 1924.

J. G. Agardh (*loc. cit.*) describes *G. asperifolia* as arising from a slender, elongate, rather thick stipe, cylindrical only at the very base, soon broadening to about 2 mm. in width, about 4–4.5 mm. long, and above about 4 mm. broad. Above, the stipe is expanded into a rather membranaceous frond, about 30 cm. long, linear lanceolate, divided with few bifurcations into similar laciniae (pinnae), each about 2–2.5 cm. broad, the angles between pinnae and main blade being rounded. The base of the frond and the stipe are smooth, but the adult frond and the pinnules (bifurcations) are beset, both on the margins and on the surfaces, with aculeae. J. G. Agardh does not venture to say whether the plant described by him is fructiferous or not, but the specimen, no. 23716 of his herbarium, which may be considered as the type (see pl. 50), shows tetrasporic sori, well developed. This specimen was collected at Santa Barbara, California, by Mrs. Bingham.

We are inclined to refer a number of specimens, in the Herbarium of the University of California, to *G. asperifolia.* They are all from southern California (Santa Barbara, San Pedro, La Jolla) where the plant seems fairly common. If we are correct, *G. asperifolia* is the same as distributed by one of us (W. A. S.) under No. CXXIII of Collins, Holden, and Setchell, as *Gigartina spinosa* var. *pinnata* Setchell, or at least the tetrasporic plant is probably *G. asperifolia.* The cystocarpic plant of this distribution may be *G. Eatoniana* J. Ag., or at least there may be some of the latter species confused under the distribution. The cystocarpic specimen in the copy at the University of California, however, seems to be *G. asperifolia,* with pinnules less contracted and thickened at the base than in *G. Eatoniana* and with a smaller type of cystocarp on relatively shorter pedicels. Our plants are beautifully and fairly symmetrically flat pinnate, both tetrasporic and cystocarpic, while J. G. Agardh's type seems ill developed and with few and unsymmetrically developed pinnae. The stipe is rather longer than usual in most of J. G. Agardh's *Armatae,* more as in *G. spinosa* Kuetzing and *G. Eatoniana* J. Ag., but this is also true in our *G. Boryi.*

10. Gigartina spinosa (Kuetz.) Harv.

Harvey, Ner. Bor.-Am., 2:177, pl. 28, *B*, 1853; J. G. Agardh, Spec. Alg., 3, 1:200, 1876, Anal. Alg., Cont. V:15, 1899; Collins, Holden, and Setchell, Phyc. Bor.-Am., A: No. XX, 1899. *Mastocarpus spinosus* Kuetzing Bot. Zeit., 1847, 24, Tab. Phyc., 17: pl. 47*a–c*, 1867; *Gigartina ornithorhynchos* J. G. Agardh, Act. Holm., 1849, Oefvers. 86, excl. var. *a*.

Gigartina spinosa is usually a rather less branched (or pinnate) plant than *G. asperifolia,* of thicker substance, and with color approaching green-purplish. The stipe is pronounced, as in *G. asperifolia* and in *G. Eatoniana.* It differs from all its nearer relatives, except *G. stiriata* (Turn.) J. Ag. from the South African (or "Cape") region, in having the fertile pinnules not only stout but also decurrent along the margin or surface on which they are borne and appressed against the blade. It differs from *G. stiriata* in not having the fertile pinnules more or less flattened and provided with aculeae. It ranges from the Monterey Bay region on the middle Californian coast to southern California (San Pedro).

11. Gigartina Eatoniana J. Ag.

Plate 51

J. G. Agardh, Anal. Alg., Cont. V:11, 1899; De Toni, Syll. Alg., 4, 5:178, 1924.

Of this species, J. G. Agardh gave neither a complete diagnosis nor any detailed description. He states that the Californian phycologists have held various views concerning it, some considering it to be a young form of *G. spinosa,* others, as a form of *G. Harveyana,* while others have held it to be the true *G. volans.* J. G. Agardh regards it as related to the South African *G. insignis,* yet the Californian plant, he says, bears the cystocarps in rather elongated marginal pinnae, and possibly several on the same pinna, while others, on the uppermost parts of pluriseriate pinnae emerging from the surface itself, are subsessile, at times topped by a sterile apiculus. The representation of this species in Herb. Agardh at the University at Lund consists of three specimens, two of them sent by Daniel C. Eaton (no. 23593), and a sterile plant, probably juvenile, sent by Mrs. Bingham from Santa Barbara. The species seems closer to *G. spinosa* than to *G. protea,* but differs from the former in being rather a thinner plant, more branched, and with the marginal cystocarps borne on slender non-decurrent pinnules. It does not seem to be common in southern California but a few specimens in the Herbarium of the University of California may be referred to it.

J. G. Agardh compares *Gigartina Eatoniana* (Anal. Alg., Cont. V:11, 1899) with *G. insignis* (Endl. et Dies.) J. Ag., of the South African region, but that species is clearly different, being thick (although fairly broad) and strictly distichous. *G. insignis* seems to belong, along with *G. disticha* (Sond.) J. Ag., with *G. pistillata* in *Eugigartina.*

SERIES B. MAGNIFOLIATAE

The plants of this series seem to represent only a further development of the more advanced members of Series A, the *Pinnatae,* in that the main expansion has broadened and no longer shows well developed pinnate branching from its margins. The marginal branching is almost entirely reduced to teeth, abbreviated fertile pinnules, or an occasional but not regular (or normal?) foliaceous proliferation. The surface pinnules are short and largely fertile, showing their tetrastichous origin in that, while they cover very largely one or both surfaces, there is always an intramarginal zone which is devoid of them. This may be present in some of the broader species of the preceding subgenus (*Chondracanthus*), presumably representing transitional forms in the general line of development. This group seems to be the climax development of the *Gigartina* assemblage in which the lateral branches are developed quadrifariously, i.e., in a tetrastichy.

Subgenus 5. CHEILOGIGARTINA

(*Radulae* J. G. Agardh, Anal. Alg., Cont. V:25, 1897, p.p., incl. also (p.p.) *Apodae,* p. 31, *Homoeopodae,* p. 32, *Brachypodae,* p. 36, *Heteropodae,* p. 38, and *Heteromorphae,* p. 41, p.p.).

In this subgenus are included the members of Series B, in which both the cystocarps and the tetrasporangial sori are borne on pinnules (or emergencies). The type species is *Gigartina californica* J. Ag.

12. **Gigartina californica** J. Ag.

Plate 52

J. G. Agardh, Anal. Alg., Cont. V:39, 1899.

The only adult specimen (no. 23933) among those referred to *Gigartina californica* by J. G. Agardh in his collection at the University of Lund is one distributed by Farlow, Anderson, and Eaton, under no. 122 of their Algae Exsiccatae Americae-borealis. It is a stout, thick, dark-red plant, with a comparatively short stipe, with a broad, smooth, sterile area on the moderately broadly cuneate base of the blade proper, above which the obovate lanceolate blade shows the thick margins bluntly serrate, narrow intramarginal smooth zones on each surface, as well as thickly placed, short, stout, appressed, wart-like, tetrasporic papillae. The whole plant is 30 cm. high and 10.5 cm. broad at its maximum breadth. The other specimen is too young to show its exact character. No. 23933 of Herb. Agardh, therefore, seems to be the plant from which J. G. Agardh drew up his description and it is represented on plate 52. No. 122 of Farlow, Anderson, and Eaton, in the copy at the University of California, is young but seems to be referable to *G. exasperata* Harv. et Bail. rather than to Agardh's plant.

The type specimen, with the blunt serrations of the margins and the closely appressed rounded or elongated verrucose surface pinnules, is evidently a tetrasporangial plant. Several specimens in the Herbarium of the University of California seem referable to *G. californica,* among them both cystocarpic and tetrasporic plants. The cystocarpic plants have marginal pinnules longer than those of the tetrasporic plants, and each pinnule usually bears a single cystocarp, crowned with one, or more commonly coronate with several aculeae. The surface pinnules in cystocarpic plants are very short, bearing usually a single cystocarp, so short stalked as to be almost sessile, and tipped by one or more short and broad aculeae.

The type locality is Santa Cruz, California, with Dr. C. L. Anderson as collector. Other specimens have been found in the vicinity of San Francisco, California.

Gigartina californica J. Ag., as Agardh remarks, has been confused with *Gigartina radula* (Esper) J. Ag., as have been *G. exasperata* Harv. et Bail. and *G. corymbifera* (Kuetz.) J. Ag. from the Pacific coast of North America as well as certain species from New Zealand, and even the species of South Africa have been confused in respect to their relationships to *G. radula.* The type of *G. radula* is the *Fucus radula* "Turner" (*in* Esper, Icon. Fuc., 5 :3, pl. 113, 1802). An examination of Esper's specimens is not possible at present, but he states that his plants were from Australia, sent to him by Dawson Turner, under the name he uses. Turner (Fuci, 1 :54, pl. 25, 1808), however, figures and describes a South African plant that seems to us to be a different one from Esper's, regretting that he cannot conserve the name applied to the plant in Herb. Banks, viz., *Fucus radula,* on account of the priority of *Fucus bracteatus* Gmelin (Hist. Fuc., 212, 1768), a plant seemingly of the East Indies. It seems impossible that the plants of Gmelin, if really more than one is to be included, can be Gigartinas. The East Indian plant of Rumphius (Herb. Amboin., 6 :186, 1750) cited by Gmelin and apparently relied upon by him to make his description complete, is described as of a pale brown. Since the only *"Agarum"* form of the East Indies in any wise suggested by the Rumphius reference is *Hydroclathrus clathratus* (Bory) M. A. Howe, we may leave this part of Gmelin's proposal as probably inconsequential. Gmelin's first reference, however, is not so easily set aside. Seba (Thesaur., 3 :192, pl. 103, figs. 2, 3, 1754) shows, in the figures of the plate quoted, so seemingly accurate a representation of Kuetzing's *Chondrodictyon capense* as to make Turner's reference of *his* plant certain. The reasonable surmise is, that *its* source was the Cape region of South Africa, since J. Christian Bay of the John Crerar

Library has kindly informed the writers that many materials of African origin were included by Seba in his museum.

The discussion now concerns Esper's publication of *Fucus radula*, evidently, from a comparison with Turner's figure, not the same plant as Turner's. Esper figures the same plant twice; as dry (fig. 1), and after soaking out (fig. 2). In both figures the intramarginal zone is very prominent, the cystocarpic papillae are short, and the cystocarps are obliquely once or more sharply apiculate, while the cystocarpic papillae seem numerous on the surfaces and fairly closely spaced in groups, but not crowded. If the type plant is really Australian, it may be one occurring there of which no specimen is available to the writers; a plant similar to or possibly identical with *G. circumcincta* J. Ag. If of the "Cape," or South African region, it may be represented by Kuetzing's *Mastocarpus incrassatus* of which only the tetrasporic plant was described. It does not seem to be the *Gigartina polycarpa* (Kuetz.) comb. nov. (Spec. Alg., 733, 1849; Tab. Phyc., 17 :13, pl. 44, 1867), which has the cystocarpic papillae so crowded as almost to eliminate the intramarginal naked zone, or *G. spathulata* J. Ag., which is pinnately branched below and which therefore might be intermediate between *Cheilogigartina* and *Chondracanthus*, or *Gigartina verrucosa* (Kuetz.) comb. nov. (*Mastocarpus verrucosus* Kuetz., Tab. Phyc., 17 :12, pl. 42, 1867) with its broader blade, cordate base, and sparse cystocarpic papillae. All these species are properly to be placed under the subgenus *Chondrodictyon*.

The reference of *Gigartina radula* to the west coast of North America began with Turner (Fuci, 1 :54, pl. 25, 1802), who places a Menzies specimen under his *Fucus bracteatus*. This specimen has not been reëxamined but seems likely to be either *G. californica* or *G. exasperata* Harv. et Bail. J. G. Agardh finally came to the conclusion (Spec. Alg., 3, 1 :203, 1876) that *G. radula* should be limited to the "Cape" species with immersed tetrasporangial sori (*Chondrodictyon capense* Kuetz.) but, in fact, he included other "Cape" species as well. The foregoing discussion of the "Cape" series therefore seemed desirable in order to elucidate this situation. Further study may show that the Esper type did really emanate from the Australian region; if so, then *G. radula* proper may be closely related to such a species as *G. circumcincta* of New Zealand. Its nearest substitute on the west coast of North America is probably *G. californica* J. Ag., which we previously (Univ. Calif. Publ. Bot., 1 :302, 1903) assumed to represent the typical form of *G. radula*. The latter now seems to be different, and, while the former is to be referred to the subgenus *Cheilogigartina*, the true *G. radula* must certainly belong to the subgenus *Chondrodictyon*.

13. **Gigartina corymbifera** (Kuetz.) J. Ag.

Plates 53 and 54

J. G. Agardh, Spec. Alg., 3, 1:202, 1876; *Mastocarpus corymbiferus* Kuetzing, Bot. Zeit., 1847, 21; Species Algarum, 734, 1849; Tab. Phyc., 17:13, pl. 46, 1867; J. G. Agardh, Spec. Alg., 2, 1:274, 1851 (sub *Gigartina ornithorhynchos*, var. *a*, J. Ag.); Spec. Alg., 3, 1:684, 1876 sub *G. papillata; Gigartina radula* f. *exasperata* Setchell *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., A: No. XVIII, 1899 (excl. syn. non-Kuetz.).

Gigartina corymbifera is a large, thick species, with a narrower to broader, obovate terminal expansion arising gregariously from an expanded holdfast (or prostrate basal portion). It averages about 30 cm. in height and from 6 cm. to 15 cm. in width, mostly entire, but is occasionally unequally bifurcate. The stipe gradually widens upward, for 6–8 cm. is smooth, both on the margins and the surfaces, before any outgrowths occur on the blade. The color is usually yellowish red to a wine red and is very distinctive in the living plants. The substance is thick and chartaceous in dried plants. The fertile pinnules are thickly scattered over both surfaces and along the upper margins, as a rule, the cystocarpic varying from short and stout to rather long and slender, mostly corymbosely branched above, with three or more blunt cystocarps each. This is the particular characteristic of the species and is well shown in the illustration of Kuetzing (*loc. cit.*). The tetrasporangial papillae are simple, stout, blunt, and short. Both cystocarpic and tetrasporic plants show a distinct naked intramarginal zone, but it is usually more marked in the cystocarpic plant.

Kuetzing's plants, two in number, are marked "Ex Herb. T.C.D.—California—Dr. Coulter" and have *"Iridaea papillata"* apparently in Harvey's handwriting. They probably came from the vicinity of Monterey Bay, whence come most of the specimens at our disposal. Some characteristic specimens are before us from Santa Barbara (Mrs. S. P. Cooper), and others, not so characteristic but possibly of this species, from the Puget Sound region. In southern California it may be readily confused with *G. Binghamiae* J. Ag. and in the north with *G. exasperata* Harv. et Bail., but both are thinner, less rigid plants and lack the corymbose cystocarpic pinnules. Its zone of abundance and of characteristic expression is the central Californian coast.

14. **Gigartina exasperata** Harv. et Bail.

Harvey and Bailey, Proc. Bot. Soc. Nat. Hist., 3:371, 1851; Bailey and Harvey, Alg. U. S. Expl. Exp., 17:162, pl. 5, 1862. *Gigartina radula* f. *exasperata* Setchell and Gardner, Univ. Calif. Publ. Bot., 1:303, 1903, p.p.

As Harvey and Bailey indicate, this species has a relatively thin and membranaceous blade for its large size. Some forms are not readily to be distinguished from young plants of *G. corymbifera,* with which we (*loc. cit.* above) earlier confused it. The adult plants may be as much as one meter high and at times nearly one-third as broad. They may be entire or unequally furcate; young plants resembling the figure of *Iridaea lapathifolia* Kuetz. (Tab. Phyc., 17: pl. 16, 1867) in aspect, but very different otherwise. There is a horizontal expanded basal portion, whence arise several erect fronds. There is a short cylindrical stipe, usually not branched, which flattens and expands gradually, narrowly cuneate, up to 2–3 cm. long, suddenly broadening into the narrowly to broadly cuneate ovate-lanceolate blade. The color is light rather than dark red. The margins are sharply serrate to slender dentate, occasionally foliiferous, with minute pinnules or even larger pinnae, at times simulating a gigantic *G. armata* or others of the *Chondracanthus* group. The surfaces of the blade, other than the narrow, naked, intramarginal zone, are covered with small, simple, prickle-like projections, giving the surface of dried plants the feeling of a sharp file or fine rasp. These projections bear the tetrasporangial sori on some plants and the cystocarps on others. The sori extend downward and in some plants are almost immersed in the frond. The cystocarps are usually single, but sometimes two or three are borne on the same short papilla, and are usually singly or doubly long-acuminate just below the apex. The antheridia cover the surface of rather slender and elongated surface papillae, and antheridial plants are thickly margined with short (1–2 cm. long) ovate-lanceolate pinnules which give it a distinctive aspect.

Gigartina exasperata grows mostly in the sublittoral belt and the larger specimens are cast ashore from deep water; hence, in all probability, its varying aspect. It extends from the west coast of Vancouver Island, B. C., south, possibly even to the San Diego region. It seems most abundant in the northerly portions of its range.

15. **Gigartina Harveyana** (Kuetz.) comb. nov.

Rhodymenia ciliata β microphylla Harvey, *in* Hooker and Arnott, Bot. Beech. Voy., 164, 1833; *Gigartina microphylla* Harvey, Ner. Bor.-Am., 2:176, pl. 28, *A*, 1853; *Mastocarpus Harveyanus* Kuetzing, Spec. Alg., 734, 1849, Tab. Phyc., 17:13, pl. 45*o–g*, 1867; *Gigartina radula* f. *microphylla* Setchell *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., A: No. XIX, 1899.

As indicated in the citations above, the first name given was *microphylla,* but only as a varietal name. *Microphylla,* however, has been the accepted specific name since 1853. The first specific name is *Harveyanus* of Kuetzing (1849), and it becomes necessary to adopt it.

Gigartina Harveyana is well illustrated, the plant depicted by Harvey (*loc. cit.*) being tetrasporic while that represented by Kuetzing (*loc. cit.*) is cystocarpic. It is to be distinguished fairly readily from all other *Cheilogigartina*-species by its long, narrow, thin blades, linear-lanceolate in shape, up to 75 or 80 cm. long and 2–8 (averaging around 3) cm. in breadth. The fronds are clustered, arising from a prostrate basal growth, very slender at first and cylindrical, then compressed and on to complanate, passing over a few cm. farther insensibly into the expanded blade. At the tip it is again gradually attenuated to a sharp point. When growing in tideways, as it commonly does, either stipe or blade, at varying heights, may be mutilated or whipped off. Proliferation ensues and new blades may arise, imitating the original in gradually attenuating into a stipe-like portion at the base, so that a semblance of branching, similar to that of *Chondracanthus* species, may (and frequently does) occur.

The intramarginal naked zone is present and may be conspicuous. The margins are beset with shorter or longer serrulations, the teeth often being curved or with short, compressed, almost foliaceous pinnules. The surface papillae are regularly and closely placed, covering the surface nearly but not quite to the margins. They are simple, short, and slender in both cystocarpic and antheridial plants, stouter in tetrasporic plants. The color is wine red, the substance of the dried plant is membranaceous-chartaceous, the surfaces rough to the touch, like a fine file, but the fresh plant is soft and velvety. The species ranges from the Puget Sound region of Washington (?) to southern California.

Gigartina Harveyana, when short, broad, and somewhat thicker than usual, might be considered to grade into *G. californica,* and, in attempting to set up only major species as was done in 1903 (see Setchell and Gardner, Univ. Calif. Publ. Bot., 1:303, 304, 1903), we reduced it as a form under the binomial *G. radula.* While all the *Gigartinae* run into perplexing and possibly intergrading forms, *G. Harveyana* is one of the most distinct species in the *Cheilogigartina* subgenus. Certain proliferous (?) states resemble *G. Boryi.*

16. Gigartina Binghamiae J. Ag.

Plate 55

J. G. Agardh, Anal. Alg., Cont. V:33, 1899; De Toni, Syll. Alg., 4, 5:186, 1924.

J. G. Agardh designates this as a beautiful species which was sent to him from Santa Barbara, California, by Mrs. Bingham. Plate 55 represents the type specimen (no. 23895) in his herbarium. It is about 24 cm. high and 9.5–10 cm. broad. It appears to be a rather young cystocarpic plant. In the Herbarium of the University of California is a series of plants which seem to belong with Agardh's type. They approach *G. corymbifera* in one direction and *G. exasperata* in another. The species is thinner and more membranaceous than *G. corymbifera,* and the papillae are simple, not corymbosely branched. The fronds are thin like those of *G. exasperata,* but not so ample in dimension, and the papillae are blunt, not so sharp as in *G. exasperata.* In other points of habit besides texture and papillae they resemble most closely *G. corymbifera.* Young plants might be mistaken for any one of the three species.

The lower young plants in plate 55 show the habit of growing in small clusters from a basal layer, the stipes being cylindrical below, becoming flattened to compressed to complanate above, with occasionally a few (two or three on a side) divaricate spinule-like branchlets, finally abruptly but not flaringly expanded into a narrower or broader obovate lamina. The color is light wine red, very similar to that of *Gigartina corymbifera* and of *G. exasperata.* The margins are smooth to serrulate, sparsely or even more thickly clad with slender, simple, fertile pinnules or papillae. An intramarginal naked zone is present, but seldom pronounced. The surfaces are sparsely to thickly covered with slender papillae, usually blunt, topped by the globular cystocarps or swollen laterally by the tetrasporangial sori into slightly raised warts. *Gigartina Binghamiae* J. Ag., while seemingly most abundant along the coast of southern California, has also been collected, in not altogether typical specimens, on the Oregon coast and in the Puget Sound region of Washington (Whidbey Island).

Subgenus 6. CHONDRODICTYON (Kuetz.)

Kuetzing, Phyc. Gen., 396, 1843, as genus, Spec. Alg., 729, 1849.

There are a few species, seemingly, properly attributed to the genus *Gigartina* and seemingly also closely related to the members of the subgenus *Cheilogigartina,* so far as the cystocarpic plant is concerned, yet, in respect of the tetrasporic plant, showing affinities to *Rhodoglossum,* in that they have the tetrasporangial sori immersed in the frond, near to the surface, but not elevated on emergences or papillae. The type of the genus, as proposed by Kuetzing, is *Gigartina bracteata* (Gmelin) *nobis,* which was determined earlier in this account to be the proper binomial for *Chondrodictyon capense* Kuetz. In his first accounts Kuetzing (*loc. cit.*) described the cystocarps as immersed in the frond, but as having the *spermatia* 4–2-parted. Later he (Tab. Phyc., 17 :6, pl. 21, 1867) recognized the tetrasporic nature of his earlier plant and correctly figured (*loc. cit.,* figs. *c, d*) the cystocarps on papillae. It may be argued that *Chondrodictyon* represents a distinct generic type, but in some species of the *Cheilogigartinae* the tetrasporangial emergence is slight and occasionally barely emergent. Two Californian species enumerated by J. G. Agardh are to be referred to *Chondrodictyon.* These are *Gigartina volans* (Ag.) J. Ag. and *G. velifera* J. Ag. The remaining species of *Chondrodictyon* are austral.

17. Gigartina volans (Ag.) J. Ag.

Plates 56 and 57

J. G. Agardh *in* C. A. Agardh, Icon. Alg. Ined., edit. nov., No. XVIII, pl. XVIII, 1846; Setchell, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., A: No. XXI, 1899; *Sphaerococcus volans* C. A. Agardh, Icon. Alg. Ined., No. XVIII, pl. XVIII, 1821.

C. A. Agardh founded this species upon specimens in Herb. Chamisso, said to have been collected in the region of the Cape of Good Hope. J. G. Agardh, in his revision of his father's "Icones Ined.," expressed the opinion that probably they came from the coast of California. In 1851, J. G. Agardh said that the type specimens were preserved in Chamisso's herbarium and that he had not seen them. In 1903, search was made in Herb. Agardh at Lund and three numbers (23602–23604) were found under *Gigartina volans,* including in all five specimens, all from Santa Cruz and all sent to J. G. Agardh by Daniel C. Eaton, of Yale University. There were cystocarpic, but no tetrasporic, specimens among them. The peculiarity of the tetrasporic plant was first noted by Setchell in the specimen distributed under No. XXI of the Phycotheca Boreali-Americana, noted above. Even in his final revision of *Gigartina* in 1899, J. G. Agardh (Anal. Alg., Cont. V :12) does not seem to have advanced farther in his knowledge and places *G. volans* in his *"Prolificantes,"* a rather ill assorted group.

Gigartina volans (Ag.) J. Ag., if we assume the west coast of North America to be its source, is not scarce, but it assumes a number of forms, some of which may be very much unlike others in what may perhaps be considered as variations due to immediate environmental differences. All the plants are thick, cartilaginous, and gregarious from a common, expanded, horizontal base. In more protected habitats, the stipes are moderately elongated, gradually more and more compressed and broadened above; finally, at about 4–8 cm. above the base, the stipe expands rather suddenly into the cuneate base of the broad blade, which may be 10–20 cm. long and 3–7 cm. or more wide. The stipe may be once dichotomous, but in the plants spoken of it is usually simple. The blades may be simple, or once or twice, even thrice, broadly furcate.

In more agitated water, surge, or tideways, the plants are usually much elongated and tend to be narrower. The stipes remain narrow, or with occasional dilations, somewhat in an elongated opuntoid fashion, reaching at times a length of 20 cm. or even 30 cm. before expanding into blades. They may also be once to several times dichotomous, and more or less sparingly provided with pinnate proliferations. The blades are usually much smaller than in the plants subjected to less stress.

While the species is fairly multiform, and all that is definitely known concerning the type comes from the original short diagnosis and figure of the two Agardhs, supplemented by C. A. Agardh's later longer description (Spec. Alg., 1, 2:266, 1822), nevertheless it is usually a fairly easily recognized species. Plates 56 and 57 show complete plants of both cystocarpic and tetrasporic types. The coarse cystocarpic papillae scattered over the surfaces and divaricate along the margins, the elongated stipes, the thick texture, and the tendency toward an opuntoid habit make it a marked plant among the *Gigartinae.* It is fairly abundant along the northern and central coasts of California, and apparently occurs occasionally in southern Oregon and in southern California (La Jolla).

18. Gigartina velifera J. Ag.

Plate 58

J. G. Agardh, Anal. Alg., Cont. V:41, 1899.

There is only one specimen of this in Herb. Agardh at Lund and plate 58 shows that this represents only the upper portion of a blade. It was sent to J. G. Agardh by Mrs. Hall without name and without locality. It was probably collected somewhere on the coast of central California. J. G. Agardh placed it, by itself, in a special tribe, the Heteromorphae. Possibly the type specimen is only a portion of the plant sent by Mrs. Hall, since the lower end shows the marks of having been removed by cutting from a larger plant. J. G. Agardh thinks of it as suggesting the habit of a certain *Laurencia pinnatifida* but with its main portion and its branches attaining an inch in breadth, and as approaching *G. volans* more closely in general appearance than any other species of *Gigartina.*

Specimens of what seem otherwise to be typical *Gigartina volans* vary toward the wavy, proliferous, and pinnate margins of *G. velifera,* and there are present, in the collections available to us, specimens which seem definitely referable to it. No. 6536, N. L. Gardner, collected from drift near the mouth of the Carmel River, in Monterey County, California, in August, 1930, has all the characters of J. G. Agardh's type plant of *G. velifera* as to undulate, proliferous margins, short foliaceous surface pinnules, etc. It is antheridial, as is also in all probability the type plant of J. G. Agardh. This sort of variation from type, i.e., foliiferous rather than papillate, is fairly characteristic of the antheridial plants of the species of *Chondracanthus* and *Cheilogigartina.* We may conclude, therefore, that *G. velifera* J. Ag. is a Californian species and may represent an antheridial plant of *G. volans* (Ag.) J. Ag. The patches of calcareous epizoa and epiphytes on the type specimen of *G. velifera* also are characteristic of *G. volans* and not so usual on other broad *Gigartinae.*

SERIES C. PALMATAE

The description of this series has been given earlier in this account, and the species placed under it, having the same general character, are so different from those of Series A and Series B as to suggest removal from the genus *Gigartina*. Series C is very closely related to *Chondrus*, as exemplified by the flat, rather broad *C. crispus* types, from which the less differentiated forms such as *Gigartina unalaschensis* (Rupr.) Rupr. are to be distinguished only by the more globular protruding cystocarps, and the occasional or frequent marginal and surface papillae. In the lack of a differentiated concentric inner pericarpic layer, the species of Series C resemble *Chondrus crispus* and differ from the species of Series A and B of *Gigartina*. There are, however, still retained in the genus *Chondrus*, and otherwise seeming properly to belong to it, species which do possess a differentiated inner pericarp. It seems best, for the present at least, to continue to retain the species of Series C within the limits of *Gigartina*.

Subgenus 7. MASTOCARPUS (Kuetz.)

Mastocarpus Kuetzing, Phyc. Gen., 398, 1843, as genus p.p. *Mammillaria* Stackhouse, Mém. Soc. Imp. Nat. Moscou, 2:55, 1809 (non *Mamillaria* Haw., 1812).

It has seemed best to use *Mastocarpus* of Kuetzing rather than *Mammillaria* Stackhouse even for a subgeneric name, since the latter has long been used for a genus of Cactaceae and has received sanction, as against the earlier *Cactus* L., among the *nomina conservanda* of the International Botanical Congress of Vienna, of 1905. The genus *Mastocarpus* of Kuetzing was seemingly founded on *M. mamillosus* (Good. et Woodw.) Kuetz., along with three other species not to be included under the *Palmatae*. Kuetzing's figures (*loc. cit.*, pl. 76, III) of the cystocarpic papilla of *M. mamillosus* and the details of its structure are excellent and show clearly the lack of an inner specialized pericarp layer.

The species of this subgenus are even more difficult of cleavage and delimitation than those of the other subgenera we have outlined under *Gigartina*. There seem to be intergradations uniting all into possibly one major species, but it seems best, because of the prominence of certain types, to attempt at least a seriation into microspecies. In 1903 (Setchell and Gardner, Univ. Calif. Publ. Bot., 1:301, 302), the attempt was made to distinguish all of them as "forms" of *G. mamillosa*, but that has not proved satisfactory. A return will now be made to, or toward, the views of J. G. Agardh of 1899, at least on the assumption that the entities outlined are microspecies, undoubtedly of uneven and varied phyletic significance, intermediates being frequent, at least seemingly so when any attempt is made to place various specimens closely among the fairly abundant material available for study.

The species of *Mastocarpus*, as subgenus, have in common the repeated dichotomy that, in its best development, gives rise to a palmate frond. The margins are usually described as swollen, but this seems rather exaggerated. The margin is rounded and often slightly enlarged.

It has a tendency to curl, so as to make one surface concave, the other convex. This is always to be seen toward the base of the blade and even throughout in the forms with narrow divisions, but is less conspicuous in the forms with very broad divisions. The margins also are free from outgrowths, or very nearly so, except in a few species, where they may occur, and even plentifully. In most plants, even where marginal papillae may seem to occur, careful examination will show that, while close to, they are not actually on the margin. Careful search has failed to reveal any tetrasporic plants of the species of this section. It may be that this type of reproduction is absent and the failure to find them, or to find descriptions of them in the literature, seems to support such a hypothesis. Individuals of both cystocarpic and antheridial plants occur in such abundance and so generally distributed, that, even if the season for tetraspore reproduction were much more limited than seems probable, it certainly is remarkable that not a single tetrasporic individual is recorded or has rewarded the careful search made for them. Even more constant and comprehensive search will continue, but at present it is impossible to postulate with satisfaction anything further than that no trace of them is known at the present time.

The species of the subgenus *Mastocarpus* are largely boreal, but two striking species are austral, viz., *G. alveata* (Turn.) J. Ag. and *G. ancistroclada* Mont., both narrow, with both margins and tips curved, representing an extreme in habit of *G. Agardhii* and *G. Jardinii* of the Pacific coast. It may seem best later to separate the two austral species under a special subgenus characterized by the involute tips. A third species, *Gigartina australis* J. Ag., from Australia, may be placed among the *Sulcatae.*

a. PACIFICAE. Cystocarps on terminal, marginal, and superficial lobes or papillae.

In this section are placed the high northern species included by Kjellman under his species *Gigartina pacifica* (Kjellman, Kongl. Sv. Vet.-Akad. Handl., 23, 8:31, pl. 1, figs. 21, 22, 1889). The plant figured by Kjellman, to include the three varieties of Ruprecht (Tange Och. Meer., 318, 1851), seems to represent only an extreme of the *Chondrus mamillosus* var. *ochotensis* Rupr., leaving the other two, var. *unalaschcensis* Rupr. and var. *sitchensis* Rupr., to be segregated as has been done by J. G. Agardh and by Yendo, as will be indicated farther on.

19. Gigartina unalaschcensis (Rupr.) Rupr.

Plate 59

Ruprecht, *in* Kjellman, Kongl. Sv. Vet.-Akad. Handl., 23, 8:31, 1889; J. G. Agardh, Anal. Alg., Cont. V:11, 1899; Yendo, Bot. Mag. Tokyo, 30:54, 1916. *Chondrus mamillosus* var. *unalaschcensis* Ruprecht, Tange Och. Meer., 318, 1851.

The first point to be noted is the spelling of the name; Ruprecht, "*unalaschcensis*," Kjellman, "*unalaschkensis*," J. G. Agardh, "*unalaschensis*," and Yendo, "*unalaskensis*." It has seemed best from every point of view to adopt the original spelling of Ruprecht.

Then comes the consideration of the species (or microspecies). Ruprecht (*loc. cit.*) compares it with the plant figured on plate 2011 of the Flora Danica, but adds that it is only half as large and much shorter stalked. The lobes are numerous, broad, obovate, overlapping one another, and divided at the broad rounded ends into many small fertile lobules. The large thick cystocarpic warts extend, at times, down along the margins and are also sparsely distributed on both surfaces of the frond. The frond is forked once below, but above the divisions are palmate. All the divisions, as well as the whole plant, are so short stalked and so broad that one sees only the expanse of the frond which obscures the base. Thus, Ruprecht describes his variety. J. G. Agardh never described the species, as he adopted it, but his main idea may be judged from the specimens in his herbarium, reproduced on plate 59, two specimens evidently determined by Ruprecht. Of these, the cystocarpic specimen to the left seems better to correspond to Ruprecht's than that to the right and it is here considered typical. The specimens retained in Herb. Acad. Sci. at St. Petersburg (or Leningrad) represent a mixture.

In attempting the difficult task of segregating specimens of *Gigartina unalaschcensis*, the writers have borne in mind the close resemblance to forms of *Chondrus crispus*. The specific cleavage is not exact, but the short, crisped, almost stipeless form, with incurved margins and numerous fairly broad lobes, with cystocarps largely on the terminal lobes but also to some extent along the margins and in patches on the surface, has been the type in mind. On plate 59, the lower specimen is undoubtedly cystocarpic, and the right-hand figure of Yendo (*loc. cit.*, p. 56, fig. 2) may represent an extreme form or may be a broad form verging toward *G. pacifica* Kjellman.

The type locality is Unalaska Island, one of the larger Aleutian chain. It has been collected at St. Michael, Alaska, within the Bering Sea, and at places along the Pacific coast of North America down to Puget Sound (Whidbey Island), and possibly even at exposed points on the northern Californian coast.

It seems to pass over into *Gigartina ochotensis* Rupr., but no typical forms of this species as illustrated by Yendo (Bot. Mag. Tokyo, 30:57, 58, fig. 4, 1916) nor anything typical of *Gigartina pacifica* Kjellm. (as figured by Kjellman, *loc. cit.*, which may be a broad form of *G. ochotensis* Rupr.) have been seen on the North American side of the Pacific Ocean, although seemingly frequent on the northerly coasts of the Asiatic side.

20. **Gigartina sitchensis** Rupr.

Ruprecht, *in* Kjellman, Kongl. Sv. Vet.-Akad. Handl., 33, 8:31, 1889; Yendo, Bot. Mag. Tokyo, 30:57, fig. 3, 1916. *Chondrus mamillosus* var. *sitchensis* Ruprecht, Tange Och. Meer., 318, 1851.

According to Ruprecht, this species is similar to the Atlantic var. *echinata,* but so short stalked as to approach the *Sphaerococcus papillatus* Ag. The shape of the frond is broad, as indicated above, and both sides are covered with papillae, which are wanting in younger fronds and on the lowest portions of the fruiting fronds. Yendo (*loc. cit.*) has given figures of two specimens from the original material in "Herb. Acad. St. Petersburg" and one shows distinctly the marginal as well as the superficial papillae. While separable with difficulty, in some of its forms, from simpler forms of *G. latissima* (Harv.) Eaton, the presence of marginal papillae seems sufficient to warrant its being kept as a microspecies.

The type locality presumably is Sitka, Alaska. The few specimens available were collected on the coasts of British Columbia and of Washington (Whidbey Island).

b. MAMILLOSAE. Cystocarpic papillae superficial, practically never marginal (apical or lateral); tips not inrolled or involute.

The *Mamillosae* differ from the *Pacificae* in that, although the papillae often seem marginal, close inspection will indicate that they are definitely just within the naked, inrolled margins or else clearly superficial. All the species show conspicuously the naked, smooth, rounded, involute margin, which seems slightly swollen. In the upper, much expanded portions of certain species the incurving of the margins is slight. In the species whose divisions are all narrow the incurved margins are conspicuous, resulting in a decidedly canaliculate frond. The tips in the *Mamillosae* are straight or nearly so, while in the *Alveatae,* of New Zealand and Tasmania, they are sharply revolute, both on the longer main branches and on the much shorter superficial pinnules.

(*a*) Stipes very short, expanded into broad, nearly plane, obcuneate divisions (*Eumamillosae*).

21. **Gigartina latissima** (Harv.) Eaton

Plate 60

Gigartina latissima Eaton, *in* J. G. Agardh, Anal. Alg., Cont. V:32, 1899. *Gigartina mamillosa* var. *β latissima* Harvey, Jour. Linn. Soc., 6:172, 1862.

J. G. Agardh says that the specimens in his herbarium, placed under this name, recall in their form and ramification and in variety the plants usually referred to *Gigartina mamillosa,* but that the segments of *G.*

latissima are much broader than those of *G. mamillosa,* although they vary in this respect. The cystocarps, scattered and sparse in *G. mamillosa,* are densely placed on the upper segments of *G. latissima,* so as to cover them closely, and are subglobose, each with a proper carpostome. In *G. mamillosa,* on the other hand, they are both more individual and more segregated, and on the lower part of the pinnules less transformed than in *G. latissima.* In the Agardh herbarium at Lund are a number of specimens, largely sent by Daniel C. Eaton from various parts of California, mostly not of the var. *latissima* Harvey, but rather with longer and more complex stipes, which seem better referred to *Gigartina cristata,* to be considered later on. The type may be considered to be the no. 23855 (see pl. 59), a Harvey specimen from Esquimault, B. C., and more particularly the upper left-hand specimen. Similar specimens, but better developed, have been collected by Setchell at Sooke, B. C., very close to the type locality of Harvey.

The stipe is short, about 1 cm. in length, broadly cuneate, expanding into a broad blade, nearly entire in simple forms, when it approaches in habit *G. sitchensis,* but lacking the strictly marginal papillae, or divided deeply into few to several broad segments, which, in turn, may be once, twice, or even more times divided, also into broad segments. The superficial papillae are short, 1–2 mm. long, slender to fairly stout, swollen above into a broadly globular cystocarp, when fertile. They are regularly and fairly closely distributed over the frond except over the basal area. The fronds may reach a length of 15 cm. and the broader divisions a breadth of 5 cm. This microspecies seems to pass over into the broader states of *G. dichotoma* Gardner, but that species, when well developed, has longer and more compound stipes. Typical forms have as yet been found only near the type locality and adjacent shores of British Columbia.

22. **Gigartina mamillosa** (Good. et Woodw.) J. Ag.

J. G. Agardh, Spec. Alg., 2, 1:278, 1851; *Fucus mamillosus* Goodenough and Woodward, Trans. Linn. Soc., 3:174, 1797 (vars. excl.).

The paper of Goodenough and Woodward was read on April 7, 1795, but the date on the title page of vol. 3 of the Transactions is 1797. From descriptions and references, it seems fairly certain that the "norm" or type of *Fucus mamillosus* is the plant represented by Morison (Hist. Oxon., 3: pl. 8, fig. 13, 1699), also, in turn, by Turner under *Fucus mamillosus* var. *echinatus* (Fuci, 4:53, pl. 218, figs. *h–m,* 1819), and the technical types to be the specimens quoted from Herb. Buddle. Assuming these figures to represent the strict taxonomic type, we may attribute the species with some definiteness to the Pacific coast of North America, but confined to the states of Oregon and Washington. *Fucus* *stellatus* Stackh., while undoubtedly to be united with *Fucus mamillosus* Good. et Woodw., from the point of view of a *"mega"* species, differs in having abundant apical, slender lobes and may be considered a separate microspecies from *Fucus mamillosus.* Nothing on the west coast of North America is exactly comparable with it except one set of specimens collected by Setchell and Parks at Ucluelet, B. C. These will be considered later.

Goodenough and Woodward diagnose their species as having a dichotomous frond, with the branches dilated upward, mamillose, tuberculiferous on both surfaces, and with acute apices. The plant, they say, is 2–5 inches high. The *"mamillae"* are all incurved and the fronds are canaliculate below, plane above.

The plant thus described is low, with definite stipe flattened above, gradually expanding into cuneate-based broader segments, 2–3 times or more forked, with the tips of the segments acute and naked. The papillae are short (1–2 mm. long), more or less curved, blunt, swollen above, when fertile, into the shortly clavate cystocarps. Thus far, only two sets of specimens, one from Westport, Washington, collected by A. S. Foster (no. 659) and the other from Seal Rocks, Oregon, collected by A. R. Sweetser (no. 35) represent this European microspecies on the Pacific coast of North America.

23. **Gigartina stellata** (Stackh.) Batters

Batters, Jour. Bot., 40 (suppl.) :64, 1902. *Fucus stellatus* Stackhouse, *in* Withering, Arr. Brit. Pl., ed. 3, 4:99, 1796, Ner. Brit. (ed. 1), fasc. 3:53, pl. 12, 1801. *Fucus crispus* var. γ *stellatus* Stackhouse, Ner. Brit. (ed. 2), fasc. 2: 20, pl. 12, 1816.

The first diagnosis, published in Withering's Arrangement, was probably not carefully drawn up, but the citation from Ray's Synopsis of a plant "apicibus stellatis" indicates the character of the species as elaborated and illustrated later by Stackhouse in both editions of the Nereis Britannica. It is evident that Stackhouse had in mind a plant similar to his *Fucus echinatus,* but with the apices not acute and simple but prolonged into a series of slender lobes. Batters (*loc. cit.*) has examined a Stackhouse specimen of this species in the herbarium of the Linnean Society and states that it is a form of *Gigartina mamillosa* (in the broader sense). Stackhouse, in his citation of figures, includes, however, undoubted forms of *Chondrus crispus.* A series of cystocarpic specimens of low stature, collected by Setchell and Parks at Ucluelet, on Barclay Sound, west coast of Vancouver Island, B. C., seems to answer the requirements of the *Fucus stellatus* Stackh., which differs from *Gigartina mamillosa* (Good. et Woodw.) J. Ag. (as restricted to typical form) in having the apices cut into "stellate" narrow divisions, normal in appearance and not pathological.

24. **Gigartina Turneri** spec. nov.

Fucus mamillosus Turner, Fuci, 4:53, pl. 218, figs. *a–c*, 1819.

G. fronde e disco orienda, deorsum moderate longe stipitata (usque ad 1–2 cm. alta), gradatim longe cuneate dilatata et in frondem, 1–3 dichotomam expansa, 8–9 cm. alta; segmentis superne longe attenuatus planis subfalcatus, superficiebus singulis binisve pinnulis 3–7 mm. altis, compressis, gracilibus (0.5 mm. crassis), arcuatis, simplicibus subpinnatisve, ornatis; angulis inter segmenta acutis, sinubus rotundis; marginibus segmentorum nudis; cystocarpiis in pinnulis quoquibus irregulariter seriatis, sessilibus aut brevipedicellatis.

As has been indicated earlier, the conception of *Fucus mamillosus* of Goodenough and Woodward seems fairly clear and has been included in this account under that name. The plant taken by Turner as the "norm" differs in having elongated superficial processes along which the several cystocarps are seriate. The divisions of the frond vary somewhat in width but are elongated, somewhat curved, and falcate. Since several specimens of the Pacific coasts of North America approximate closely these characters, it seems best to propose a microspecies to contain them and to dedicate it to this most able and discerning English phycologist of the early nineteenth century.

The microspecies proposed under the name *Gigartina Turneri* seems to stand between *G. mamillosa* (as limited to type) and the narrow canaliculate forms which J. G. Agardh grouped under *G. Batrachopus* (*non* Bory), of which more will be indicated later on, under *G. Agardhii*. The habit is definitely plane, but narrow forms approach more and more the canaliculate segments of *G. Agardhii,* and in these the stipe is more complex. *Gigartina Turneri,* typically from the south coast of England, seems confined on our coasts to southern California, while *G. Agardhii* is much more abundant on the coasts of central California. *G. Turneri, G. Agardhii,* and *G. Jardinii* lead toward the *Alveatae* of New Zealand and Tasmania.

(*b*) Stipes fairly short, simple, expanded into simple obovate blades, rounded or somewhat acute or once or more slightly forked at the tip. (*Papillatae*).

The species referred are two, *Gigartina papillata* (Ag.) J. Ag. and *G. obovata* J. Ag., both seemingly confined to the coasts of Pacific North America. In their larger sizes, the *Papillatae* seem to approach smaller plants of the *Cheilogigartina* group, but their margins are of the *Mastocarpus* type.

25. **Gigartina papillata** (Ag.) J. Ag.

Plate 61

J. G. Agardh, *in* Icon. Alg. Inedit. Car. Ad. Ag., ed. 2, XIX, pl. XIX, 1846; Tilden, Am. Alg., 3: no. 221, 1898; *Sphaerococcus papillatus* C. A. Agardh, Icon. Alg.

Inedit., XIX, pl. XIX, 1821; *Gigartina papillata* var. *subsimplex* Setchell, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., 9: no. 425, 1898 (non *Mastocarpus papillatus* Kuetzing, Tab. Phyc., 17: pl. 45, figs. *a, b,* 1867).

The plate of C. A. Agardh and the specimens in Herb. Agardh (no. 23883) at Lund, shown on plate 61, agree, but the attribution of the specimens to Oahu of the Sandwich Islands seems inconsistent. On the specimen in Herb. Agardh is an inscription: "E. mari atlantico, Chamisso." Both specimens and plate agree perfectly with specimens from the Pacific coast of North America. J. G. Agardh (Spec. Alg., 3, 1 :684, 1876) refers specimens from the Golden Gate (San Francisco), California, to *G. papillata* and the same type of plant is still to be found there. Since Chamisso visited this locality, it is to be suspected that this may be the type locality.

This microspecies is distinguished by being relatively simple and showing little of the digitate character of the *Mamillosae.* The stipes are short and either simple or once (or rarely twice) dichotomous. The expanded portions are also simple, often unsymmetrically notched at the more or less truncate summit, or, very rarely, split once nearly to the base. The usually simple obovate, truncate, or abruptly pointed blade has naked margins, and its surfaces, except at the base, are covered with regularly but thickly placed, short, simple papillae bearing a single slightly elongated, blunt cystocarp. There are few specimens of characteristic form other than from San Francisco north to Dillon's Beach (at the entrance to Tomales Bay) on the central Californian coast.

26. Gigartina obovata J. Ag.

Plate 62

J. G. Agardh, Anal. Alg., Cont. V:25, 1899.

The specimens in Herb. Agardh at Lund are two in number (under no. 23840) and are represented on plate 62. They appear to be more or less battered forms, and consequently proliferous, of a microspecies either identical with or certainly very close to *Gigartina papillata.* J. G. Agardh states that he formerly placed them under his *G. Jardinii,* but they are much broader and less sulcate than in his type of that species (see pl. 65). They both occurred among Berggren's specimens from the Golden Gate (San Francisco), California, probably also the home and type locality of *G. papillata.* They have the same tendency to branch dichotomously below but, probably owing to the pounding of the waves, the margins are torn, and somewhat pinnate proliferations have resulted on some of the divisions, though not on others. From an inspection of J. G. Agardh's types and comparison with a large series of plants from the type locality of both species, it seems impossible to separate *G. obovata* from *G. papillata,* even as a microspecies. In fact, J. G.

Agardh originally seems to have placed *G. obovata* as a variety under *G. papillata* (*fide* label in his handwriting on no. 23840), but later (Anal. Alg., Cont. V: 33, 1899) through his removal of *G. papillata* from his *"Mamillosae"* to his *"Radulae"* (as "G. *papillosa*," misprint!), the relationship was evidently lost sight of.

(*c*) Stipes elongated ramose and often proliferous (from the surfaces), ending above in one or more broad (?), cristate or elongated dichotomous, flat blades (*Dichotomae*).

27. **Gigartina cristata** (Setchell) comb. nov.

Plate 63

Gigartina papillata forma *cristata* Setchell, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., 9: no. 426, 1898.

G. fronde e disco orienda, breviter usque ad longe et frequenter ramoso-stipitata, superne in laminas, cuneato-flabellatas, margine superne cristatas, abeunte; marginibus inferne involutis, superne fere planis, nudis; papillis in laminas superficialibus, curtissimis, apice in cystocarpiis depresso-globosis usque ad deformibus tumescentibus.

The plants of this proposed microspecies vary both in the complexity of the stipe and in the matter of breadth of the laminae and the submarginal (or possible adnately marginal) foliose proliferations. Narrower forms resemble Turner's figure of *Fucus mamillosus* (Fuci, 4: pl. 218, fig. *c*, 1819), but broader forms resemble some forms of *Chondrus crispus* in general habit. There is a tendency to confuse short and simple stiped forms with some of those of *G. latissima*, and of narrow forms and more sulcate with *G. Agardhii*, but the cristate lobes on the upper margins distinguish it from the one and the plane fronds distinguish it from the other.

The type locality is Pyramid Point, Monterey County, California, but the microspecies extends from Puget Sound (Whidbey Island, Washington) to southern California (Orange County). It seems to be most plentiful and characteristic along the coasts of central California.

28. **Gigartina dichotoma** Gardner

N. L. Gardner, Univ. Calif. Publ. Bot., 13: 333, pl. 59, 1927.

Typical plants of this species may be known by the tendency of the blades to be elongated and to be conspicuously 3–4 times dichotomous, the divisions, while plane, being relatively narrow. The stipes may be narrow, or once to several times dichotomous. The cystocarps are very shortly pedicellate, small, and ovoid. They are distributed sparsely, but in patches. The plants are of the upper sublittoral or lower littoral, in somewhat sheltered localities of growth.

Besides the plants from the type locality at Duxbury Reef, Marin County, California, a number of specimens, possibly of the same species, but less elongated and with fewer dichotomies, are present from Moss Beach, in San Mateo County, and from Point Sur in Monterey County, California.

(*d*) Slender plants of repeated dichotomies, deeply sulcate from the base to the tips; tips not inrolled; pinnules superficial, rather long, compressed to flattened, arcuate, with irregularly seriate cystocarps. (*Sulcatae.*)

29. **Gigartina Agardhii** nom. nov.

Plate 64

Gigartina Batrachopus J. G. Agardh, Anal. Alg., Cont. V:24, 1899 (*non* Bory); *Gigartina papillata* forma *dissecta* Setchell, *in* Collins, Holden, and Setchell, Phyc. Bor.-Am., 9: no. 427, 1898; *Gigartina mamillosa* var. *vulgaris* Harvey, Jour. Linn. Soc., 6:172, 1862? *Fucus mammillosus* var. *incurvatus* Turner, Fuci, 4:53, pl. 218, figs. *n*, *o*, 1819?

G. fronde e disco basali orienda, angusta, repetite dichotoma, superne moderate expansa, sublineari, sulcata, apicibus rotundatis planisque; pinnulis gracilibus, plus minusve compressis, longioribus, cystocarpia irregulariter seriata lateralia ferentibus.

The type specimen was collected at Pyramid Point, Monterey County, California, in the mid-littoral zone and cotypes were distributed under no. 427 of the Phycotheca Boreali-Americana. It is well represented by the specimens of *Gigartina Batrachopus* J. Ag. (*non* Bory) in Herb. Agardh at Lund and reproduced on plate 64. It is fairly well separated from the other microspecies and ranges along the coast from central California (Fort Ross), where it is plentiful, to southern California (San Simeon) and even to Laguna, where it seems less abundant and less typical.

The *Gigartina Batrachopus* J. Ag. (*loc. cit.*) cannot be the *Gigartina Batracopus* Bory (Voy. Coq., 153, 1829, and Atlas, pl. 19, fig. 2, 1826) since it is so unlike his figure, and both Paul Hariot (Mission Sci. du Cap Horne, 5:70, 1889) and M. A. Howe (Mar. Alg. Peru, 105, 1914) have examined the type and find its structure more like that of an *Ahnfeldtia* or a *Gymnogongrus.*

30. **Gigartina Jardinii** J. Ag.

Plate 65

J. G. Agardh, Spec. Alg., 3, 1:200, 1876; Anal. Alg., Cont. V:25, 1899.

J. G. Agardh first (*loc. cit.*, 1876) describes this species as having a subcanaliculate frond, plane, linear, subpinnately decompound with the elongated linear segments narrowed toward the base, truncate or dentate at the apex, with lingulate-lanceolate proliferations from both surfaces and margins and bearing a single submuticous cystocarp below their apices. The species is credited to California and is placed in a group with *G. microphylla* and *G. spinosa,* i.e., among the subpinnate species of his "*Papillatae.*" Later (*loc. cit.,* 1899) he admits having placed two forms under *Gigartina Jardinii,* one of which he removes to his *G. obovata.* He now places what he considers to be the true *G. Jardinii* near *G. Batrachopus* in his "*Mamillosae,*" a relationship which seems more natural. Nos. 23800 and 23804 and 23805 represent this modified conception in Herb. Agardh at Lund. The specimen, whence the original description was drawn, is apparently his no. 23800 and is no. 154 of Mr. Ed. Jardin, collected at Monterey in 1855. Later specimens are from Santa Barbara, collected by Mrs. Bingham.

These specimens are all so close to the *Gigartina Batrachopus* J. Ag. (*G. Agardhii* Setch. et Gard.) that they certainly seem to be inseparable, even as microspecies. The branching is more subdichotomous than dichotomous, but not truly pinnate as J. G. Agardh set forth. The pinnules appear to be exclusively superficial. Certain elongated and slightly broader forms of *G. Agardhii* have been placed under this name in the Herbarium of the University of California, on account of the elongated foliaceous pinnae. These are, however, largely if not exclusively superficial or at least slightly intramarginal in origin, and are much exaggerated from the types of both *G. Jardinii* J. Ag. and *G. Batrachopus* J. Ag. If *G. Agardhii* (*G. Batrachopus* J. Ag.) is restricted to the regularly dichotomous forms and *G. Jardinii* is reserved for those elongated, irregular subdichotomous, approaching subpinnate forms, then it may be possible to retain the latter as a microspecies.

Since the survey of the genus *Gigartina,* particularly in respect of the Pacific North American species of the genus, has compelled examination of all the material of the genus accessible; and since the arrangement proposed differs in detail and placing of emphasis from that of J. G. Agardh of 1899, it seems desirable, before closing the account, to attempt to place all the species possible in their subgenera and with relation to their varying geographical distribution. In this way, the details of difference between the arrangement proposed and that of J. G. Agardh will be more readily evaluated and a general indication, at least, given of the suggestions underlying them. The basis is the Californian species (and microspecies) which represent all except one of the subgenera proposed. Through the kindness of Mr. R. M. Laing, of Christchurch, New Zealand, and through his letters, papers, and a generous sharing of his specimens, our experience has been broadened; through the kindness of the late Dr. Otto Nordstedt, the Californian types of both the Agardhs were studied at Herb. Agardh at Lund; and recently, through the kindness of Professor Harald Kylin, photographs of types were obtained. Through specimens collected along the coast of South Africa during a journey around the world in 1926–27, and through the rich collections in the Herbarium of the University of California, there has been opportunity to examine specimens of the great majority of the species attributed to the genus. There are somewhere about 14 species, however, still remaining, which seem likely to belong to the genus; but these must be studied from the type specimens before it can be determined definitely, first, whether they belong to the genus *Gigartina* or not, and second, what their relationship is to the other species.

Certain matters connected with distribution of the members of the subgenera become apparent and seemingly significant.

1. *Eogigartina* is both boreal and austral (European, east American, northeast Asian, west South American, Australasian, and South African).

2. *Mesogigartina* seems confined to the eastern Pacific Ocean region. One species only is North Pacific, 2 species are west South American, while 2 species are from New Zealand or its subantarctic islands.

3. *Eugigartina* is also well represented australly, with only 2 species (out of 12) boreal.

4. *Chondracanthus* has 2 species of Atlantic distribution, both practically boreal, 12 species North Pacific (10 being Californian), and 8 species austral.

5. *Cheilogigartina* has 5 species, all Pacific North American.

6. *Chondrodictyon* has 1 (or 2) species boreal (California) and at least 10 (–12?) austral species.

7. *Mastocarpus* is largely boreal, with about 14 species (or microspecies) in the north Atlantic and north Pacific (*Mamillosae*) while the 3 austral species (*Alveatae* 2 and *Sulcatae* 1) are confined to New Zealand and southeast Australia.

The following tentative list indicates the distribution of the recognized autonomous species of *Gigartina* among the subgenera and in general the iconography of each.

GIGARTINA Stackhouse (1809)

SERIES A.—PINNATAE

Subgenus 1. EOGIGARTINA

(*a*) SLENDER PLANTS

1. *G. acicularis* (Wulf.) Lamour. (Kuetz., Tab. Phyc., **18**: pl. 1, 1868.) S. Eur., Florida, Brazil.
2. *G. tenella* Harv. (Okamura, Icon. Jap. Alg., **1**: pl. 33, figs. 1–8, 1908.) Japan.
3. *G. intermedia* Sur. (Suringar, Alg. Jap., pl. 17, *B*, 1870.) Japan.
4. *G. Chapmanni* (Hook. f. et Harv.) J. Ag. (Laing and Gourlay, Trans. N. Z. Inst., **60**: pl. 6, fig. 29, 1929.) New Zealand.

(*b*) ROBUST PLANTS

5. *G. divaricata* Hook. f. et Harv. (Laing and Gourlay, *loc. cit.*, pl. 17, fig. 30, 1929.) New Zealand (Campbell Is.).
6. *G. tuberculosa* (Hook. f. et Harv.) Grun. (Laing and Gourlay, *loc. cit.*, fig. 26, 1929; M. A. Howe, Mar. Alg. Peru, pl. 40, figs. 12–17, pl. 41, 1914.) New Zealand (Auckland Is.). Pac. S. Am. (Peru to Fuegia).
7. *G. falcata* (Hering) J. Ag. (Kuetzing, Tab. Phyc., **18**: pl. 3, figs. *d, e*, 1868.) S.W. Europe.

Subgenus 2. MESOGIGARTINA

(*a*) SLENDER PLANTS

8. *G. serrata* Gardner. (Gardner, Univ. Calif. Publ. Bot., **13**: pls. 60–62, 1927.) Pac. N. Am. (south).

(*b*) ROBUST PLANTS

9. *G. glomerata* M. A. Howe. (M. A. Howe, *loc. cit.*, pl. 29; pl. 40, figs. 1–11, 1914.) Pac. S. Am. (Peru).
10. *G. fastigiata* J. Ag. (Kuetz., Tab. Phyc., **17**: pl. 63, figs. *a, b*, 1867, sub *Chondrus scabiosus.*) S. Africa.
11. *G. Kroneana* Rabenh. (Laing and Gourlay, *loc. cit.*, figs. 5*a*, 5*b*; pl. 7, fig. 30, 1929.) New Zealand (Campbell Is.).

Subgenus 3. EUGIGARTINA (*Gigartina* Stackhouse, 1809)

(*a*) SLENDER, SLIGHTLY COMPRESSED

12. *G. pistillata* (Gmel.) Stackh. (Kuetzing, Tab. Phyc., **18**: pl. 1, figs. *a, b*, 1868; Harvey, Phyc. Brit., **2**: pl. 232, 1849.) S.W. Eur.
13. *G. Lessonii* (Bory) J. Ag. (M. A. Howe, Mar. Alg. Peru, pl. 37, 1914.) Pac. S. Am. (Peru, Chile).
14. *G. Chamissoi* (Mert.) J. Ag. (C. Agardh, Icon. Alg. Ined., pl. 6, 1820, sub *Sphaerococcus Chamissoi*; Kuetzing, Phyc. Gen., pl. 75, II, 1843, sub *Chondracanthus chamissoi* and Tab. Phyc., **17**: pl. 66, figs. *a–d*, 1867, sub *Chondroclonium chamissoi.*) Pac. S. Am. (Peru, Chile).
15. *G. livida* (Turn.) J. Ag. (*vera!*). (Turner, Fuci **4**: pl. 254, 1819, sub *Fucus lividus;* Laing and Gourlay, *loc. cit.*, figs. 11, 12, 36, 1929.) New Zealand.

16. *G. canaliculata* Harv. (Harvey, Ner. Bor.-Am., 2: pl. 27, *C*, 1853.) Pac. N. Am.
17. *G. clavifera* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 9, 32–35, 1929.) New Zealand.
18. *G. Muelleriana* nom. nov. (Kuetzing, Tab. Phyc., 19: pl. 16, 1869, sub *G. flabellata* J. Ag. (1851) non *G. flabellata* Kuetzing, Spec. Alg., 751, 1849, *q. v.* Tab. Phyc., 18: pl. 5, figs. *a*, *b*, 1868.) S. Australia.
19. *G. Binderi* Harv. Tasmania.
20. *G. aculeifera* Zan. (orth. prop. restit. e "*G. aciculifera*" Zan.) (Kuetzing, Tab. Phyc., 17: pl. 68, figs. *c*, *d*, 1867, sub *Chondroclonium corniculatum*.) Tasmania.
21. *G. congesta* Zan. Tasmania.

(*b*) BROADER, THINNER, COMPLANATE

22. *G. decipiens* Hook. f. et Harv. (Laing and Gourlay, *loc. cit.*, figs. 17, 18, 40–43, 1929.) New Zealand.

(*c*) BROADER, ROBUST, COMPRESSED

23. *G. pinnata* J. Ag. (*vera!*). (Kuetzing, Tab. Phyc., 19: pl. 17, 1869.) S.E. Australia.
24. *G. disticha* Sond. (Kuetzing, Tab. Phyc., 19: pl. 18, figs. *a*, *b*, 1869.) W. Australia.

(*d*) BROADER, COMPLANATE, BUT THICK

25. *G. Wehliae* Sond. (Naturwiss. Ver. in Hamburg, Abh. 5, 2: pl. 4, 1871.) S. and S.E. Australia.
26. *G. crassicaulis* (*Ag.*) comb. nov. (*Sphaerococcus crassicaulis* C. Agardh, Spec. Alg., 1, 2:273, 1822; Harvey, Phyc. Austr., 2: pl. 68, 1859, sub *G. pinnata*, non J. Ag.). S. Australia.
27. *G. insignis* (Endl. et Dies.). Schmitz. S. Africa.
28. *G. insidiosa* J. Ag. S. Australia (*vera!*).

Subgenus 4. CHONDRACANTHUS (Kuetz., as genus)

29. *G. Teedii* (Roth) Lamour. (Kuetzing, Tab. Phyc., 17: pl. 66, 1867.) S. Eur., S. Amer. (Brazil), Japan.
30. *G. elegans* Grev. (M. A. Howe, Bull. Torr. Bot. Club, 57: pl. 37, fig. 1, 1930.)
31. *G. macrocarpa* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 6, 7, 8, 31, 1929; Kuetzing, Tab. Phyc., 17: pl. 67, figs. *c*, *d*, 1867?) New Zealand.
32. *G. protea* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 13, 14, 37, 38, 1929.) New Zealand.
33. *G. polyglotta* J. Ag. New Zealand (western shores). (Not seen.)
34. *G. marginifera* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 15, 16, 29, 1929.) New Zealand.
35. *G. angulata* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 24, 25, 46, 1929.) New Zealand.
36. *G. stiriata* (Turn.) J. Ag. (Turner, Fuci, 1: pl. 16, 1808, sub *Fucus stiriatus*, and Laing and Gourlay, *loc. cit.*, figs. 24, 25, 46, 1909.) S. Africa.
37. *G. Chauvinii* (Bory) Mont. (Bory, Voy. Coq., Atlas, pl. 20, fig. 1, 1826, sub *Sphaerococcus Chauvinii* var. *a*, and M. A. Howe, Mar. Alg. Peru, pl. 28, 1914.) Pac. S. Am. (Pac. N. Am.?)
38. *G. Boryi* Setch. et Gard. (See plates 48, 49; Bory, Voy. Coq., Atlas, pl. 20, fig. 2, sub *Sphaerococcus Chauvinii* var. *β*.) Pac. S. Am. and Pac. N. Am.

39. *G. echinata* Gardner. (Gardner, Univ. Calif. Publ. Bot., 13: pls. 63, 64, 1927.) Pac. N. Am. (S. California).
40. *G. leptorhynchos* J. Ag. (See plate 46.) Pac. N. Am.
41. *G. Farlowiana* J. Ag. (See plate 47.) Pac. N. Am.
42. *G. armata* J. Ag. (See plate 47.) Pac. N. Am.
43. *G. asperifolia* J. Ag. (See plate 50.) Pac. N Am.
44. *G. spinosa* (Kuetz.) Harv. (Kuetzing, Tab. Phyc., 17: pl. 47*a–c*, 1867, sub *Mastocarpus spinosus*, and Harvey, Ner. Bot.-Am., 2: pl. 28, *B*, 1853.) Pac. N. Am.
45. *G. Eatoniana* J. Ag. (See plate 51.) Pac. N. Am.

SERIES B. MAGNIFOLIATAE

Subgenus 5. CHEILOGIGARTINA

(*a*) BLADES THICK, CARTILAGINOUS, CORIACEOUS

46. *G. californica* J. Ag. (See plate 52.) Pac. N. Am.
47. *G. corymbifera* (Kuetz.) J. Ag. (See plates 53 and 54; Kuetzing, Tab. Phyc., 17: pl. 46, 1867, sub *Mastocarpus corymbiferus*.) Pac. N. Am.

(*b*) BLADES THIN, CHARTACEOUS-MEMBRANACEOUS

48. *G. exasperata* Harv. et Bail. (Bailey and Harvey, Alg. U. S. Expl. Exp., 17: pl. 5, 1862). Pac. N. Am.
49. *G. Harveyana* (Kuetz.) Setch. et Gard. (Harvey, Ner. Bor.-Am., 2: pl. 26, *A*, 1853, sub *G. microphylla*, and Kuetzing, Tab. Phyc., 17: pl. 45, figs. *c-g*, 1867, sub *Mastocarpus Harveyanus*.) Pac. N. Am.
50. *G. Binghamiae* J. Ag. (See plate 55.) Pac. N. Am.

Subgenus 6. CHONDRODICTYON (Kuetz., as genus)

51. *G. bracteata* (Gmel.) Setch. et Gard. (Seba, Thesaurus, 3: pl. 103, figs. 1–3, 1758; Kuetzing, Tab. Phyc., 17: pl. 21, sub *Chondrodictyon capense*, pl. 43, sub *Mastocarpus bracteatus*, 1867.) S. Africa.
52. *G. incrassata* (Kuetz.) comb. nov. (Kuetzing, Tab. Phyc., 17: pl. 41, 1867, sub *Mastocarpus incrassatus*.) S. Africa.
53. *G. Hystrix* (Ag.) comb. nov. (C. A. Agardh, Spec. Alg., 1, 2:223, 1822, sub *Grateloupia Hystrix*; Kuetzing, Tab. Phyc., 17: pl. 40, figs. *c*, *d*, 1867, sub *Mastocarpus radula*.) S. Africa.
54. *G. Kuetzingii* nom. nov. (Kuetzing, Tab. Phyc., 17: pl. 45, figs. *a*, *b*, 1867, sub *Mastocarpus papillatus*, non *Sphaerococcus papillatus* C. Ag.) S. Africa.
55. *G. polycarpa* (Kuetz.) Setch. et Gard. (Kuetzing, Tab. Phyc., 17: pl. 44, 1867, sub *Mastocarpus polycarpus*, misprinted *polycystus*, Tab. Phyc., 17: pl. 16, 1867, sub *Iridaea lapathifolia*.) S. Africa.
56. *G. spathulata* J. Ag. (*non* Kuetzing, Tab. Phyc., 17: pl. 45, figs. *a*, *b*, 1867.) S. Africa.
57. *G. verrucosa* (Kuetz.) Setch. et Gard. (Kuetzing, *loc. cit.*, pl. 42, 1867, sub *Mastocarpus verrucosus*.) S. Africa.
58. *G. volans* (Ag.) J. Ag. (See plates 56 and 57; C. A. Agardh, Icon. Alg. Ined., 2: pl. 18, 1821, sub *Sphaerococcus volans*.) Pac. N. Am.
59. *G. velifera* J. Ag. (See plate 58.) Pac. N. Am.

60. *G. fissa* (Suhr) J. Ag. (Suhr, Flora, 19: pl. 3, fig. 26, 1836, sub *Iridaea fissa.*) S. Am. (Cape Horn.)
61. *G. lanceata* J. Ag. (Laing and Gourlay, Trans. N. Z. Inst., 62: pl. 16, figs. 1–6, 1931.) New Zealand.
62. *G. atropurpurea* J. Ag. (type rather of *Chondracanthus?*) (Laing and Gourlay, *loc. cit.*, pl. 17, 1931.) New Zealand.
63. *G. apoda* J. Ag. (Laing and Gourlay, *loc. cit.*, figs. 7–10 and pl. 18, 1931.) New Zealand.
64. *G. grandifida* J. Ag. New Zealand (Chatham Is.).
65. *G. rubens* J. Ag. New Zealand (west coast).
66. *G. circumcincta* J. Ag. (Laing and Gourlay, *loc. cit.*, pl. 19 and figs. 11, 12, 1931.) New Zealand.
67. *G. radula* (Esp.) J. Ag. (Esper, Icon. Fuci, 5: pl. 113, 1802, sub *Fucus radula.*) Australia.
68. *G. longifolia* J. Ag. (Laing and Gourlay, *loc. cit.*, pl. 19*a*, and figs. 13–15, 1931.) New Zealand.
69. *G. orbitosa* J. Ag. New Zealand?
70. *G. gigantea* J. Ag. New Zealand (Chatham Is.), Australia, Tasmania.
71. *G. nitens* J. Ag. S. Australia.

SERIES C. PALMATAE

Subgenus 7. MASTOCARPUS (Kuetz., p.p., as genus)

a. PACIFICAE

72. *G. unalaschcensis* (Rupr.) Rupr. (See plate 14; Yendo, Bot. Mag. Tokyo, 30: fig. 2, 1916?) Atl. and Pac. N. Am.; Asia (north).
73. *G. pacifica* Kjellm. (Kjellman, Kongl. Sv. Vet.-Akad. Handl., 23: no. 8, pl. 1, figs. 21, 22, 1889.) N.E. Asia.
74. *G. ochotensis* Rupr. (Yendo, *loc. cit.*, fig. 4, 1916; Okamura, Icon. Jap. Alg., 5: pl. 247, fig. 9, 1928.) N.E. Asia.
75. *G. sitchensis* Rupr. (Yendo, *loc. cit.*, fig. 57, 1916.) N. Pac. N. Am.

b. MAMILLOSAE

(*a*) *Eumamillosae*

76. *G. latissima* (Harv.) Eaton (See plate 60). Pac. N. Am.
77. *G. mamillosa* (Good. et Woodw.) J. Ag. (Morison, Hist. Oxon., 3: pl. 8, fig. 13, 1699, and Turner, Fuci, 4: pl. 218, figs. *h*-*m*, 1819, sub *Fucus mammillosus* var. *echinatus.*) W. Eur. and Pac. N. Am.
78. *G. stellata* (Stackh.) Batters (Stackhouse, Ner. Brit., pl. 12, 1801.) W. Eur. and Pac. N. Am.
79. *G. Turneri* Setch. et Gard. (Turner, Fuci, 4: pl. 218, figs. *a*-*c*, 1819, sub *Fucus mammillosus.*) W. Eur. and Pac. N. Am.

(*b*) *Papillatae*

80. *G. papillata* (Ag.) J. Ag. (See plate 61; C. A. Agardh, Icon. Alg. Med., pl. 19, 1821, sub *Sphaerococcus papillatus.*) Pac. N. Am.
81. *G. obovata* J. Ag. (See plate 62.) Pac. N. Am.

(*c*) *Dichotomae*

82. *G. cristata* (Setch.) Setch. et Gard. (See plate 63.) Pac. N. Am.
83. *G. dichotoma* Gardner. (Gardner, Univ. Calif. Publ. Bot., 13: pl. 59, 1927.) Pac. N. Am.

(*d*) *Sulcatae*

84. *G. Agardhii* Setch. et Gard. (See plate 64.) Atl. and Pac. N. Am.
85. *G. Jardinii* J. Ag. (See plate 65.) Pac. N. Am.
86. *G. australis* J. Ag. S. Australia.

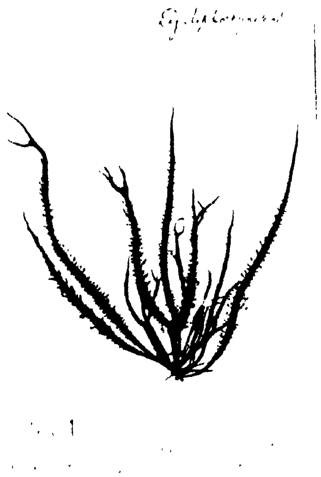
c. ALVEATAE

87. *G. alveata* (Turn.) J. Ag. (Turner, Fuci, 4: pl. 239, 1819, sub *Fucus alveatus*, and Laing and Gourlay, Trans. N. Z. Inst., 60: figs. 20, 21, 45, 1929.) New Zealand.
88. *G. ancistroclada* Mont. (Montagne, Voy. au Pôle Sud, pl. 7, fig. 4, 1842–1845, and Laing and Gourlay, *loc. cit.*, figs. 22, 23, 1929.) New Zealand, S. Australia, Tasmania.

EXPLANATION OF PLATES

PLATE 46

Gigartina leptorhynchos J. Ag. Type sheet, Herb. Agardh



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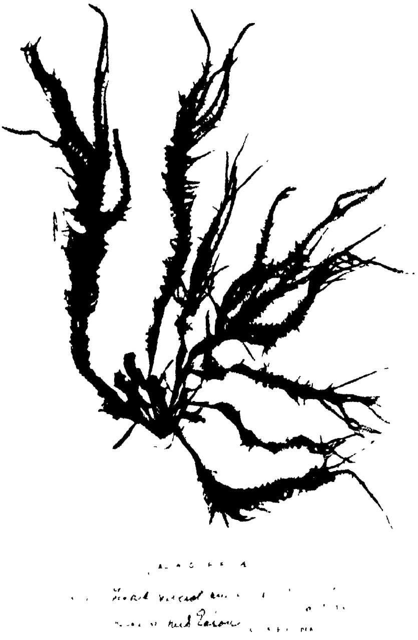

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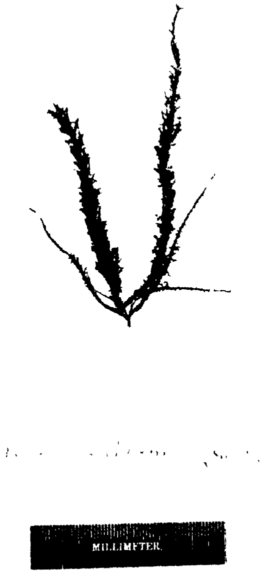

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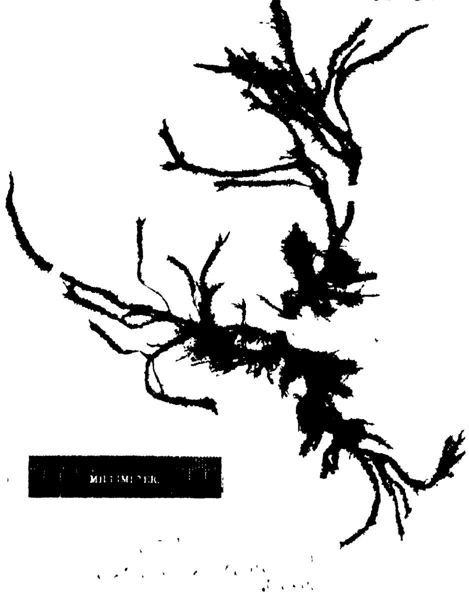
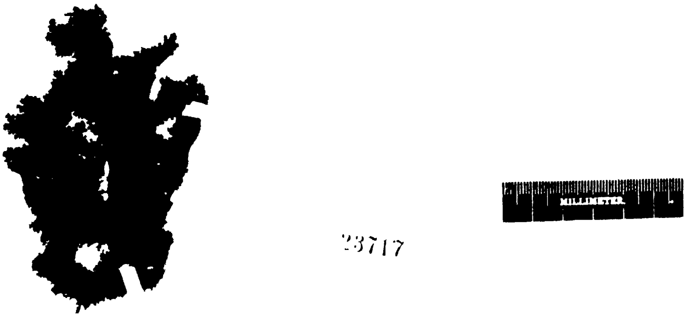


PLATE 47

1. *Gigartina Farlowiana* J. Ag. Type specimen, Herb. Agardh, no. 23717.
2. *Gigartina armata* J. Ag. Type specimen, Herb. Agardh, no. 23714.


MILLIMETER.
23717

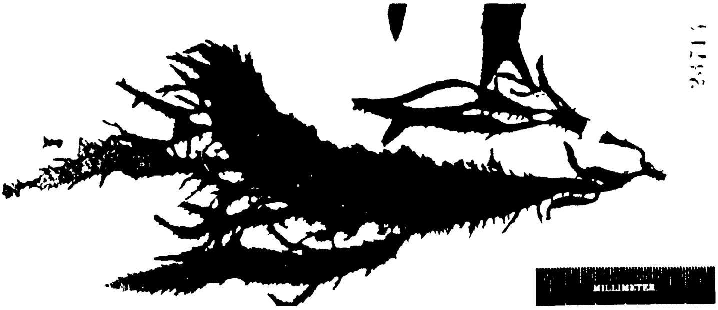

2371
MILLIMETER.

PLATE 48

Gigartina Boryi Setch. et Gard. Type specimen of cystocarpic plant, Herb. Univ. Calif.

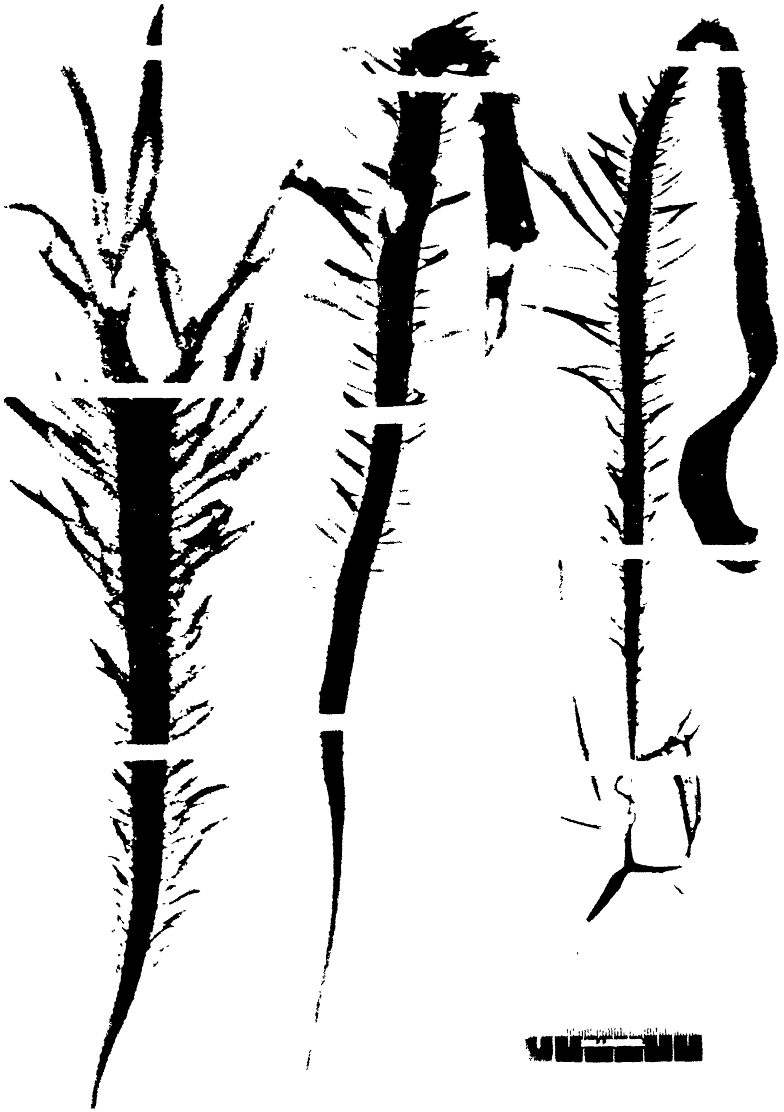


PLATE 49

Gigartina Boryi Setch. et Gard. Type specimen of tetrasporic plant, Herb. Univ. Calif.

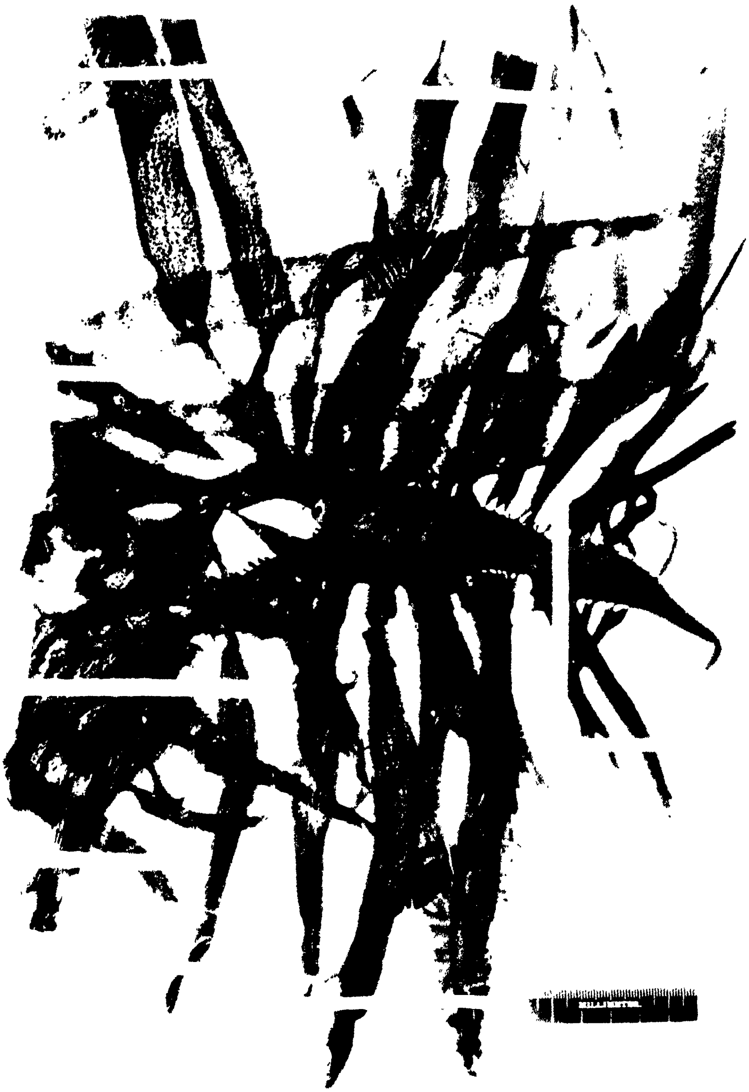


PLATE 50

Gigartina asperifolia J. Ag. Type specimen, Herb. Agardh.

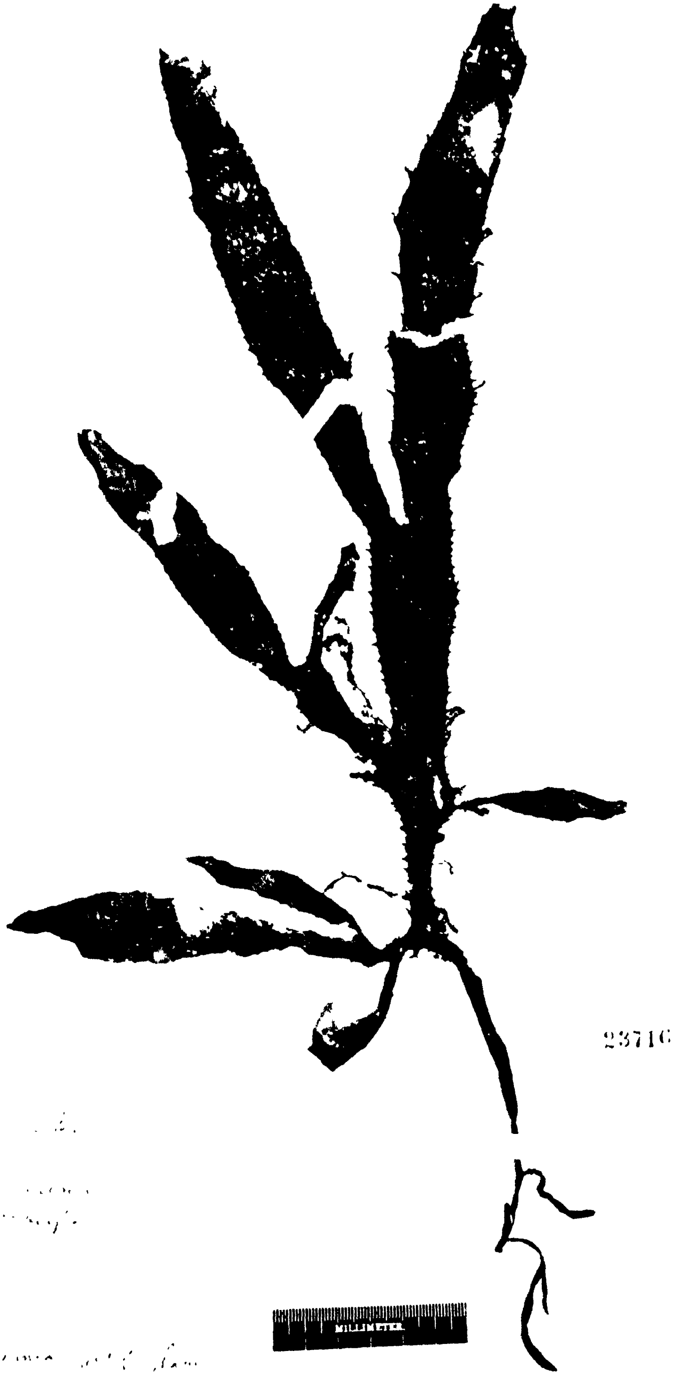
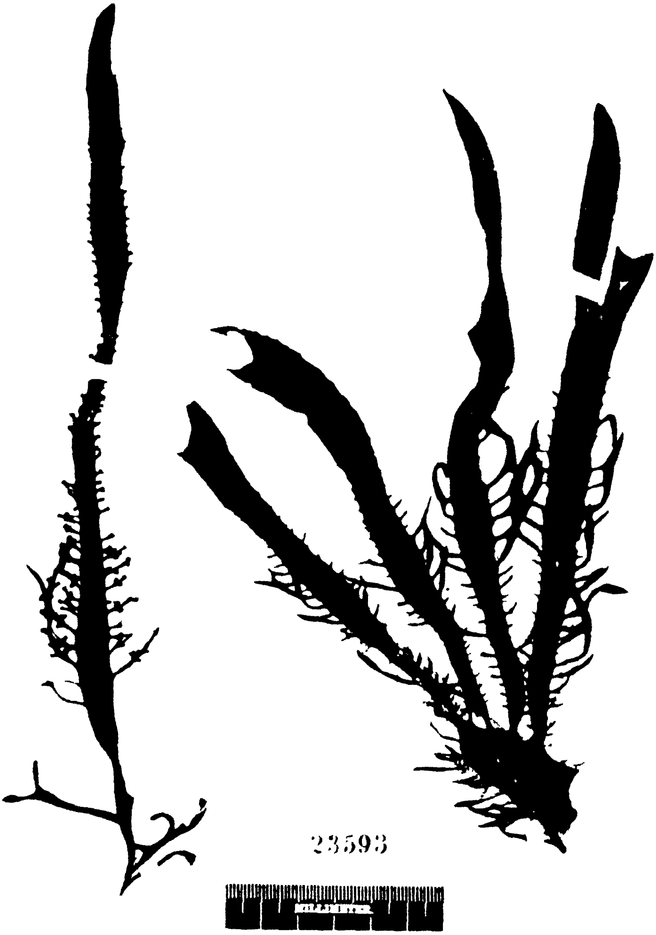
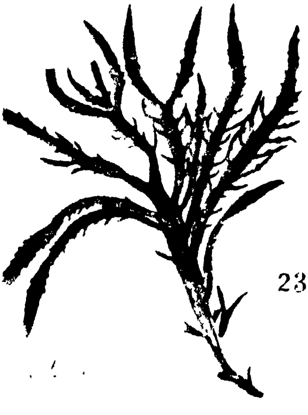

23716
MILLIMETER

PLATE 51

Gigartina Eatoniana J. Ag. Type sheet, Herb. Agardh.



23593

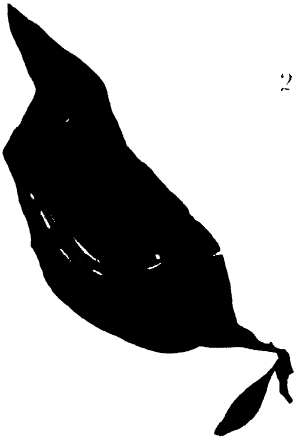


23594

PLATE 52

Gigartina californica J. Ag. Type sheet, Herb. Agardh.

23934



23933

PLATE 53

Gigartina corymbifera (Kuetz.) J. Ag. Cystocarpic plant, Herb. Univ. Calif.

PLATE 54

Gigartina corymbifera (Kuetz.) J. Ag. Tetrasporic plant, Herb. Univ. Calif.

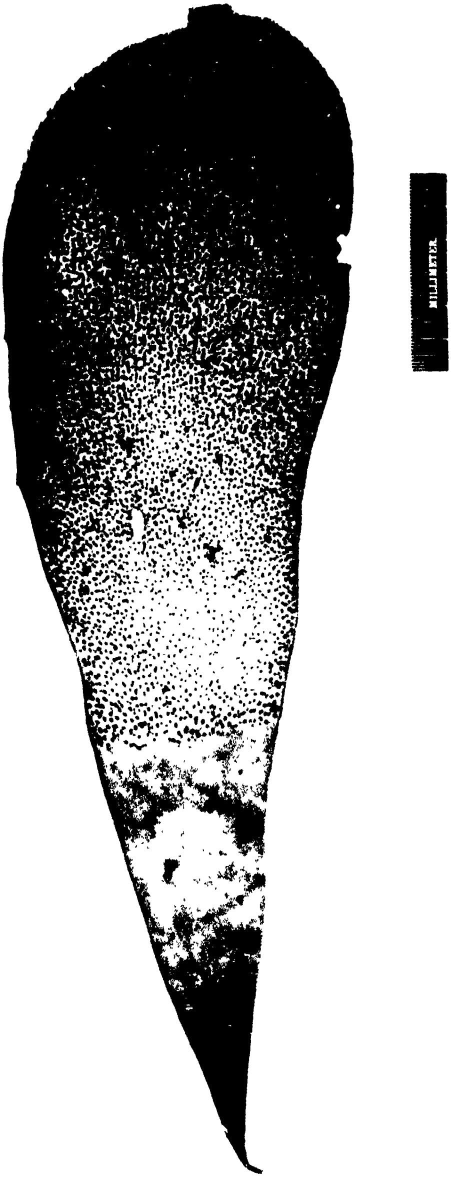
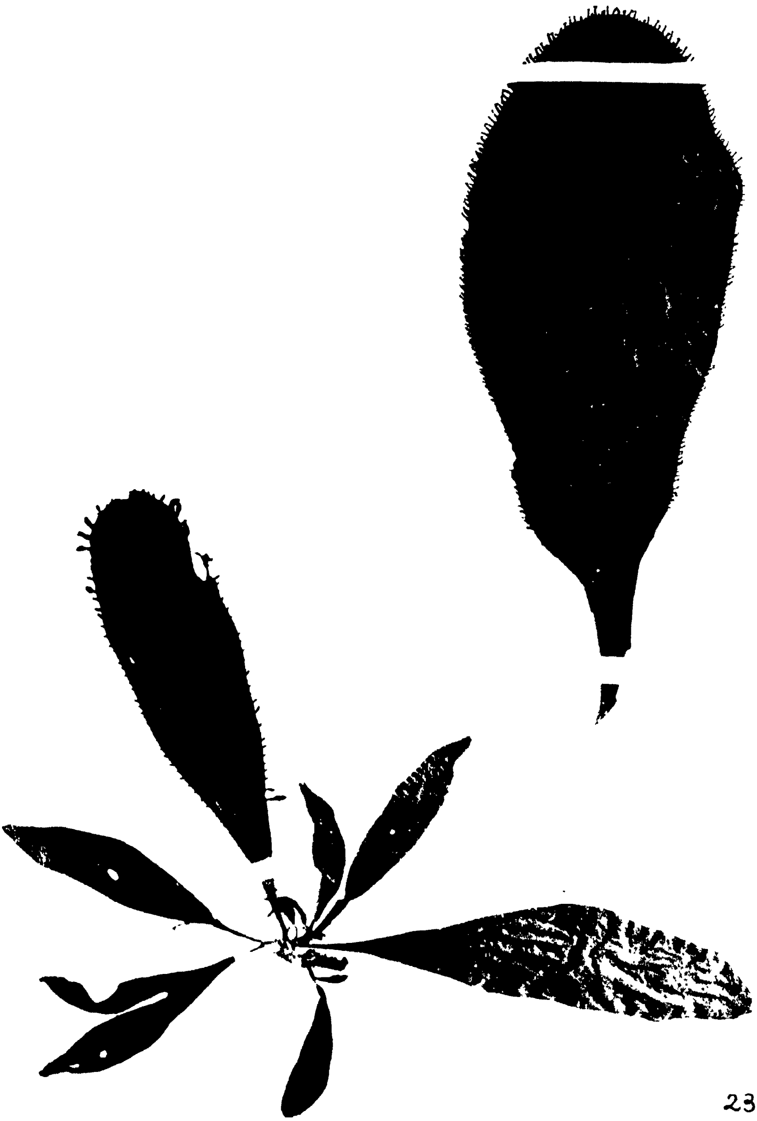

MILLIMETER

PLATE 55

Gigartina Binghamiae J. Ag. Type sheet.



23895

PLATE 56

Gigartina volans (Ag.) J. Ag. Cystocarpic plant, Herb. Univ. Calif.

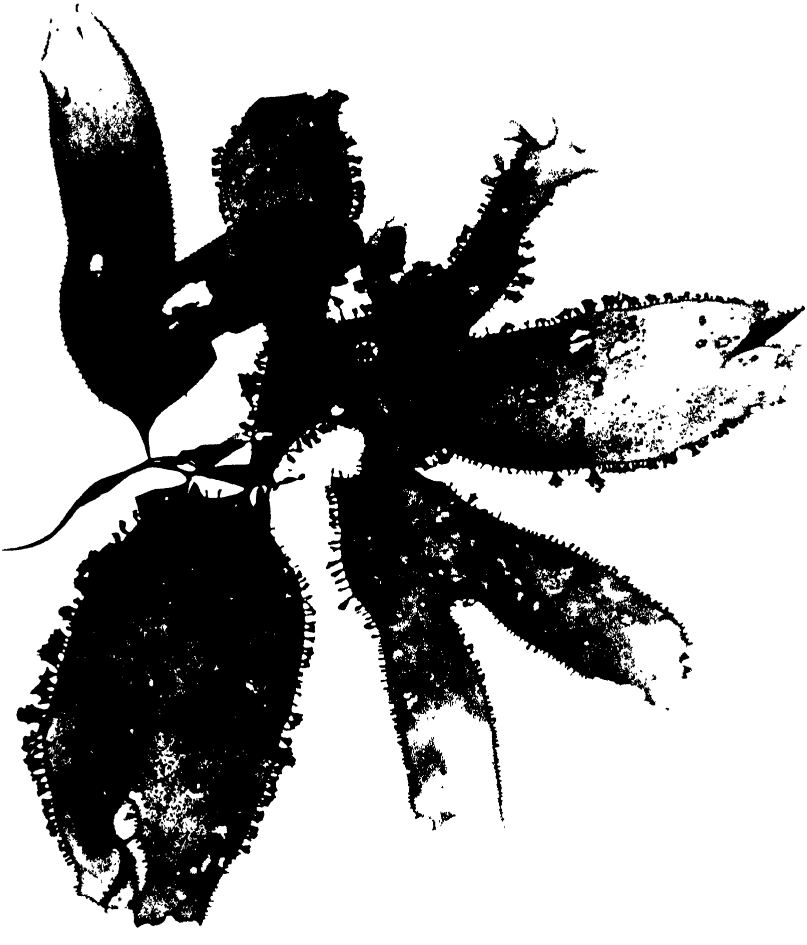


PLATE 57

Gigartina volans (Ag.) J. Ag. Tetrasporic plant, Herb. Univ. Calif.

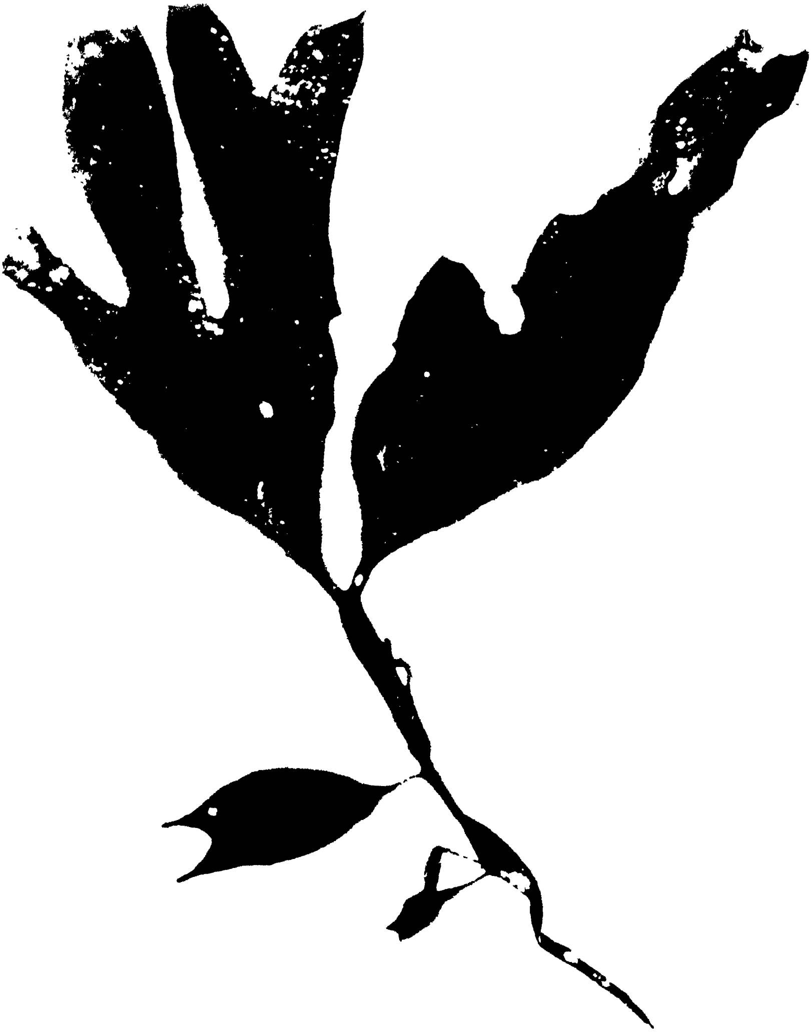
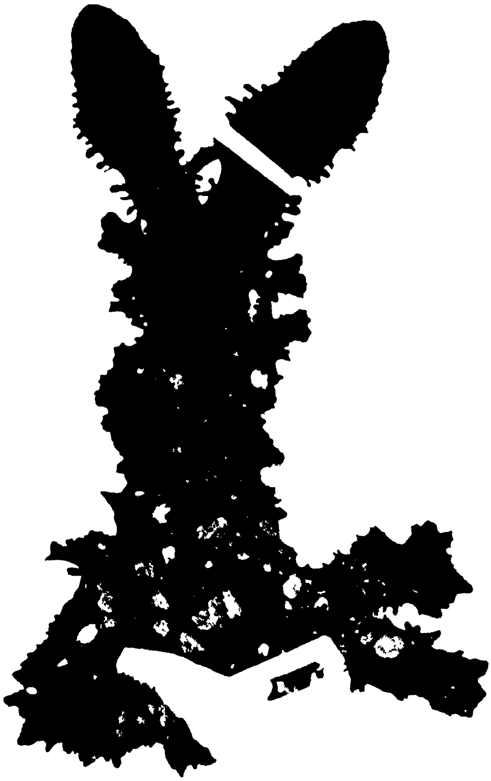


PLATE 58

Gigartina velifera J. Ag. Type specimen, Herb. Agardh.



2394

PLATE 59

Gigartina unalaschcensis (Rupr.) Rupr. Specimens in Herb. Agardh.

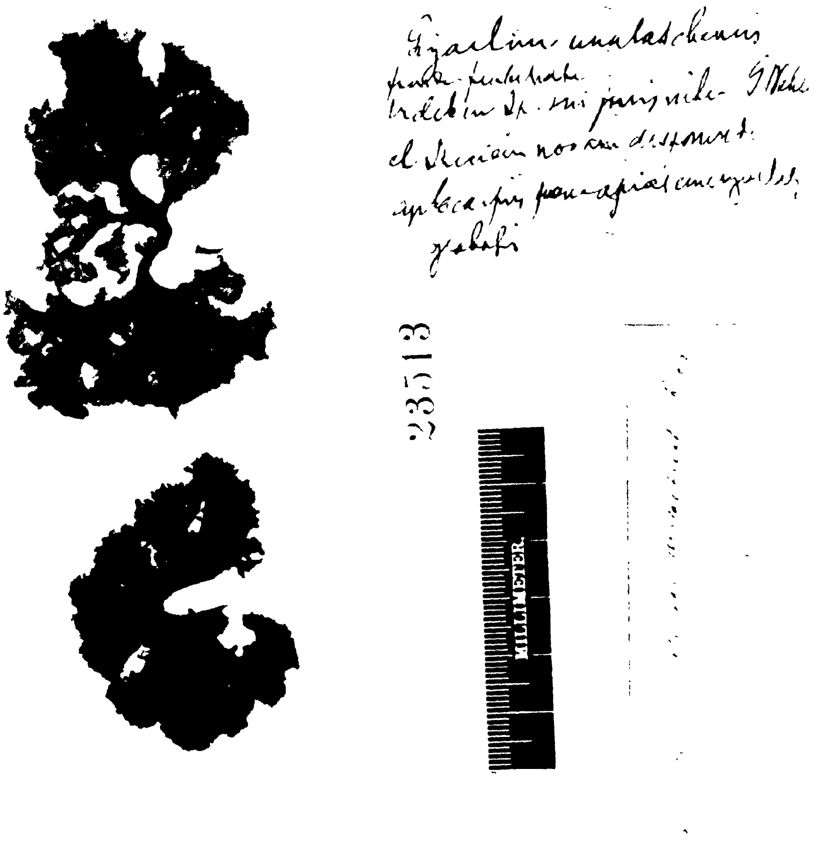
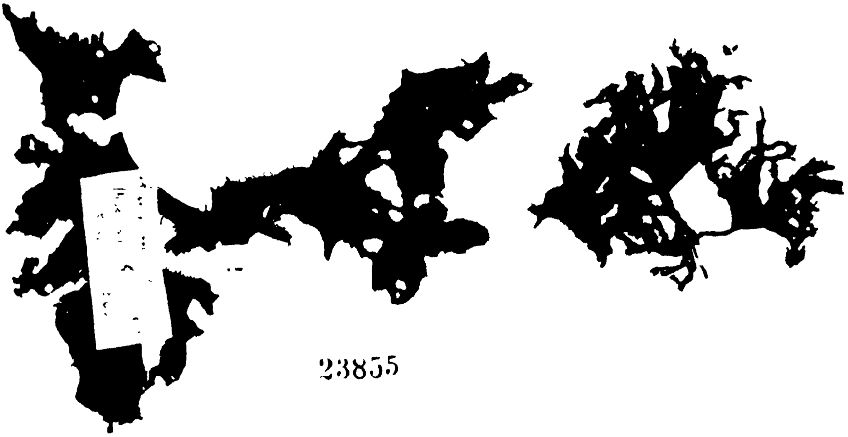
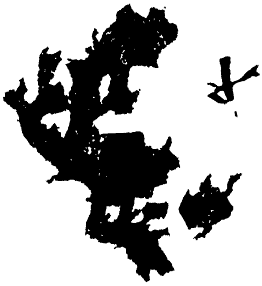

Gigartina unalaschcensis
23513
MILLIMETER

PLATE 60

Gigartina latissima (Harv.) J. Ag. Sheets in Herb. Agardh.



23855



23856

PLATE 61

Gigartina papillata (Ag.) J. Ag. Type sheet, Herb. Agardh.

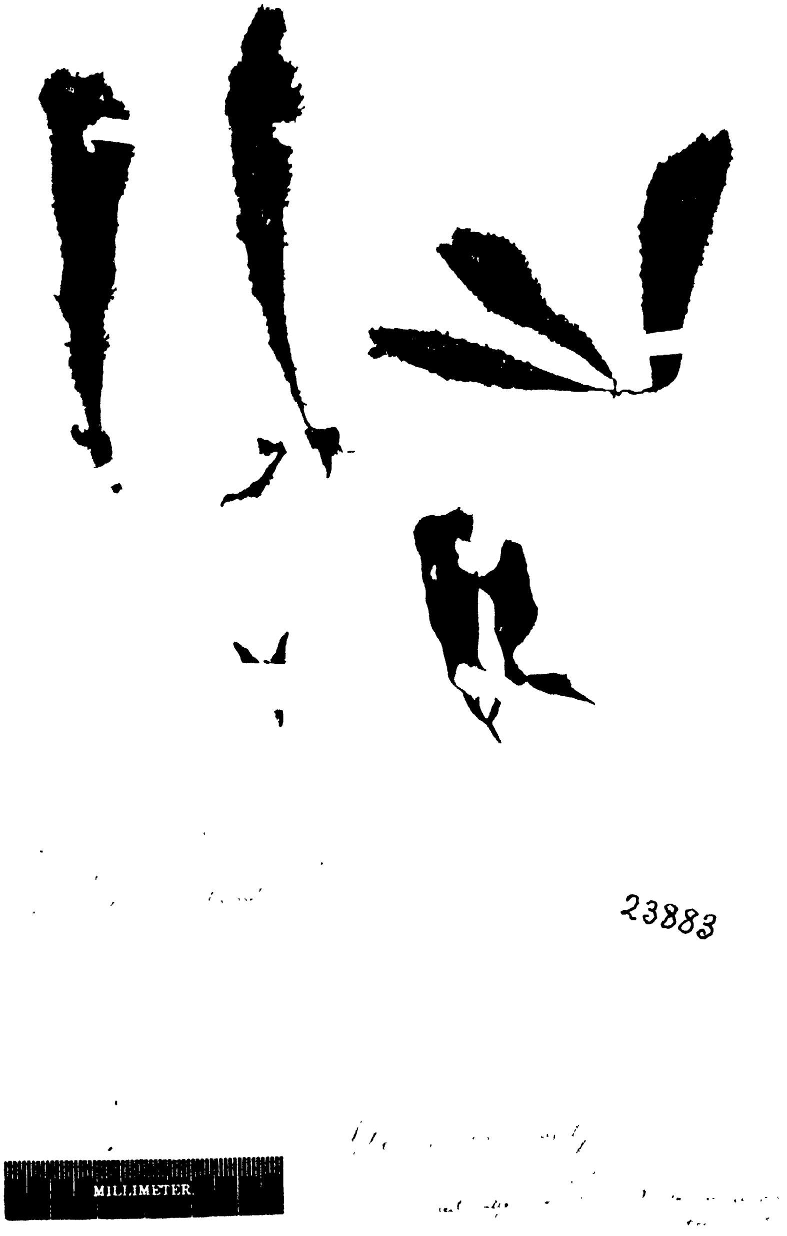

23883
MILLIMETER

PLATE 62

Gigartina obovata J. Ag. Type sheet, Herb. Agardh.

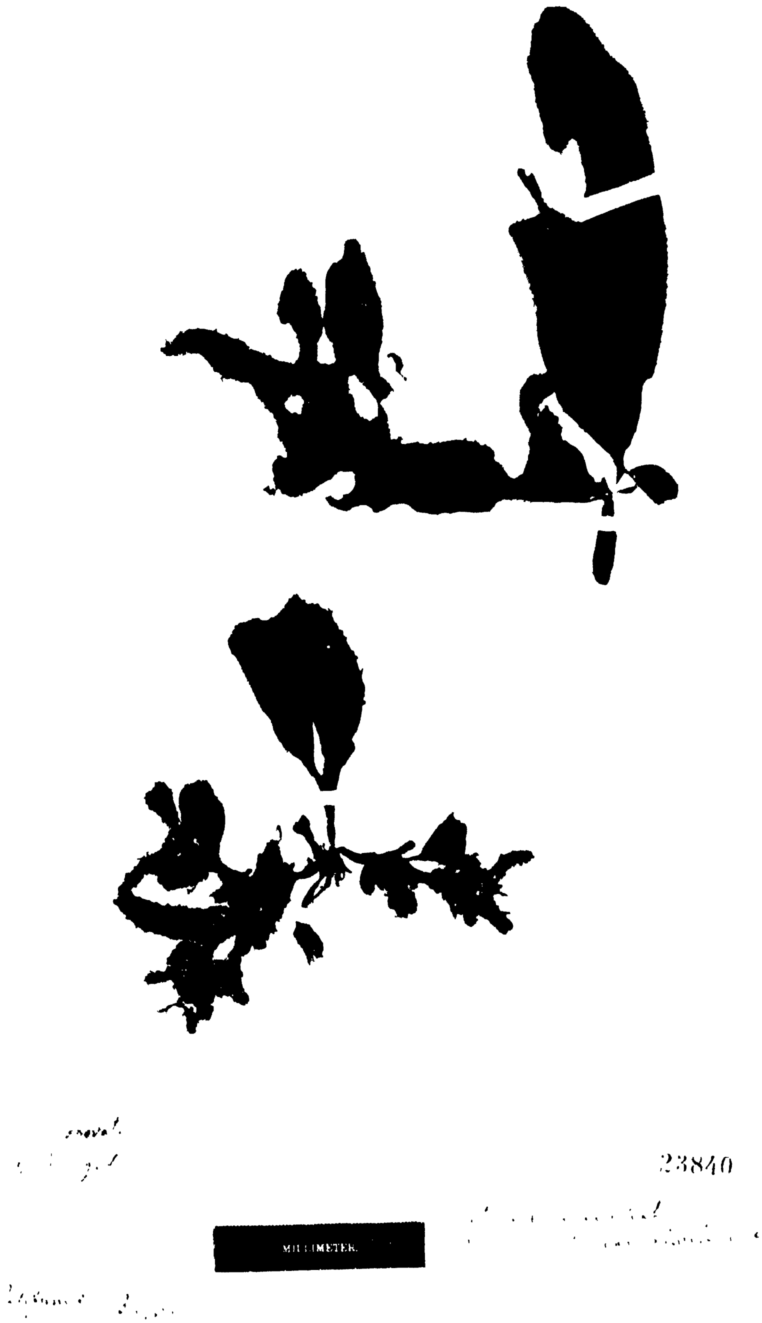

23840
MILLIMETER.

PLATE 63

Gigartina cristata (Setchell) Setch. et Gardn. Type specimen, Herb. Univ. Calif.

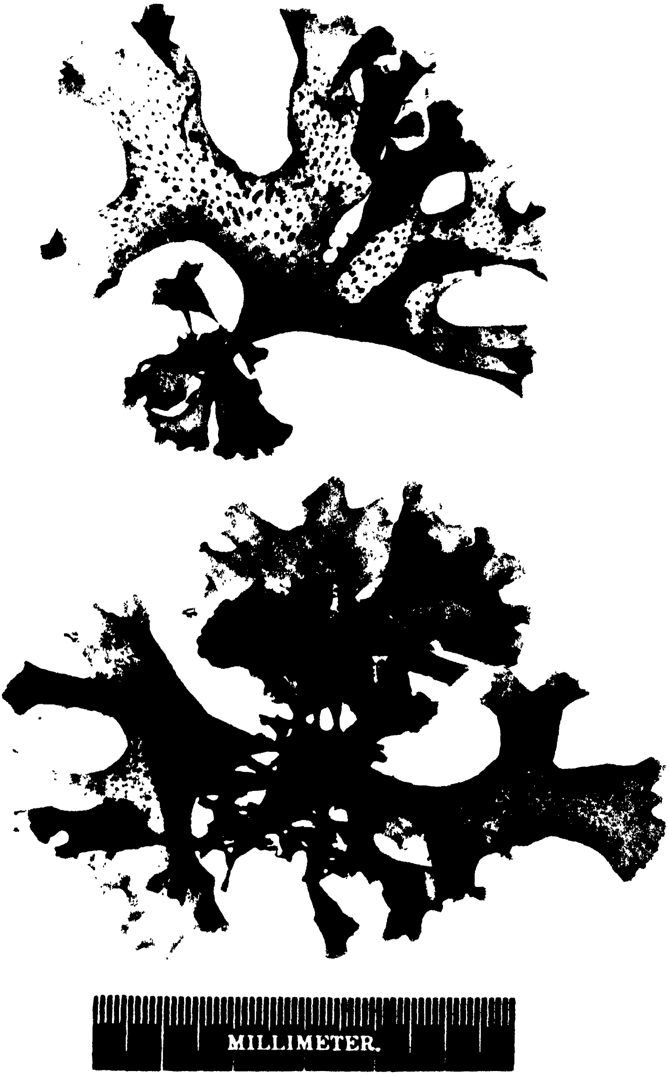

MILLIMETER.

PLATE 64

Gigartina Agardhii Setch. et Gard. Type sheet of *G. Batrachopus*, Herb. Agardh.

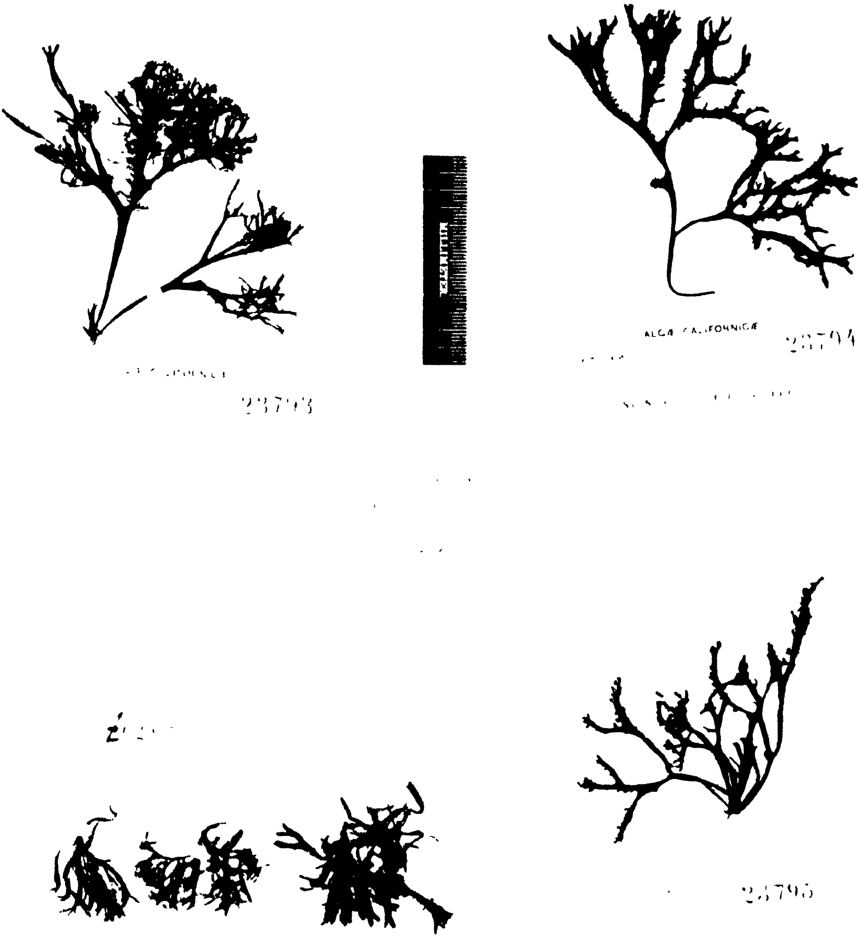
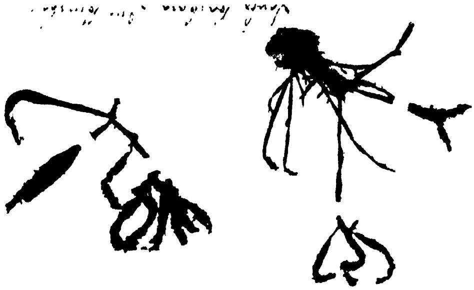

23793
ALGÆ CALIFORNICÆ
23794
23795

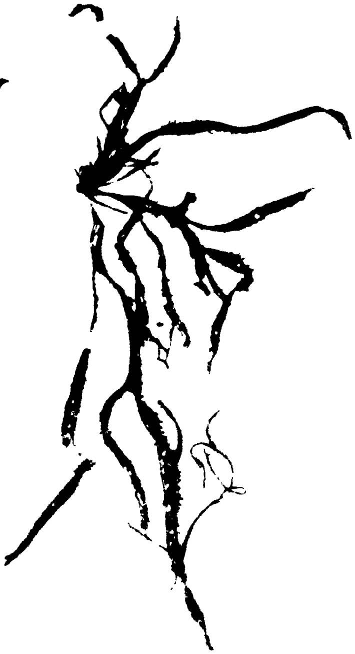
PLATE 65

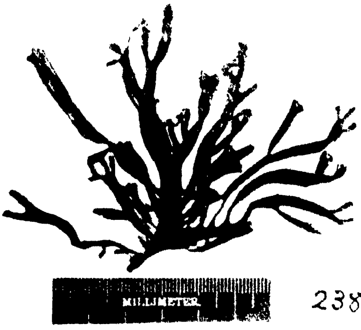
Gigartina Jardinii J. Ag. Type sheet, Herb. Agardh.

23804



23805





23800

INTERSPECIFIC HYBRIDIZATION IN NICOTIANA

XIV. THE CYTOLOGY OF F_1 GLUTINOSA × TOMENTOSA

BY

I. ELVERS

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN BOTANY
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INTERSPECIFIC HYBRIDIZATION IN NICOTIANA

XIV. THE CYTOLOGY OF F_1 GLUTINOSA × TOMENTOSA

BY

I. ELVERS

SINCE THE FIRST DESCRIPTION of the cytology of the amphidiploid *Nicotiana* hybrid *"digluta"* (Clausen and Goodspeed, 1925; Clausen, 1928) three other interspecific hybrids with doubled chromosome number have been found in this genus and studied cytologically: *N. tabacum* × *N. rustica* (Rybin, 1927), *N. tabacum* × *N. sylvestris* (Rybin, 1929), and *N. rustica* × *N. paniculata* (Lammerts, 1929, 1931, 1932; Singleton, 1928, 1932). Recently two additional *Nicotiana* amphidiploid hybrids in the cultures of the University of California Botanical Garden have been reported (Goodspeed, 1933*b*, p. 651): *"diglutosa"* (*N. glutinosa* × *N. tomentosa*) and *"disualovii"* (*N. suaveolens* × *N. Bigelovii*). *Diglutosa* has the lowest chromosome number of all the amphidiploid hybrids that have so far been obtained in *Nicotiana,* both the parents being 12_{II} species. So far as the chromosome number of the parental species is concerned, the origin of *"diglutosa"* corresponds to that postulated for *tabacum,* that is, as derived from 12_{II} species (Clausen, 1932, p. 128). The hybrid between the modern species *glutinosa* and *tomentosa* is therefore of some special interest from the cytotaxonomic point of view (Goodspeed, 1933*b*, p. 652). A brief account of the cytology of the diploid hybrid between *glutinosa* and *tomentosa* will here be given; the amphidiploid and some of its derivatives will be dealt with in a later paper. Some attention will also be given here to the nature of the homology exhibited by the chromosomes involved.

The hybrid between *N. glutinosa* and *N. tomentosa* has only been reported once (McCray, 1932, p. 622). Previous attempts to cross these species in the University of California Botanical Garden have failed. However, by using a new race of *N. glutinosa,* collected in the wild state near Lima, Peru, as female parent, this hybrid was readily made. Among the F_1 plants, one was conspicuous because of its high degree of fertility, and a cytological examination showed that it possessed 24_{II}. This amphidiploid, called *"diglutosa,"* corresponds in mode of origin to *"digluta"* (see Clausen, 1928, p. 180) and it is probable that, as in *"digluta,"* the chromosome doubling occurred in an early zygote division.

In external morphology the diploid and amphidiploid are much alike, the latter being distinguished chiefly by its fertility. At anthesis, the anthers are empty and shrunken in the diploid but well filled in the amphidiploid hybrid. In general the latter is somewhat more vigorous vegetatively.

In floral characters the two are much alike and show the influence of both parents. Thus, the flowers are not so extremely bilabiate as those of *N. glutinosa* but show about the same degree of zygomorphism as those of *N. tomentosa.* The filaments, however, are all of approximately the same height and are symmetrically disposed in the flowers, while in both parents they approach the didynamous condition found in some Scrophulariaceae, being gathered together on the dorsal side of the flower, two longer, two medium-short, and the fifth one shortest. The extreme exsertion of the anthers above the corolla, so typical of *N. tomentosa,* is not found in the hybrids. The lobes of the calyx are intermediate in length between the very long ones of *N. glutinosa* and the short ones of *N. tomentosa.* The leaves show very markedly the *glutinosa*-like petiolate leaf. McCray states that her hybrid possessed sessile leaves like *N. tomentosa.* Although the plants she describes were not full grown, and therefore the typical leaf characters may not have been fully expressed, yet the sharp distinction between a sessile and a long-petioled leaf in the two sets of hybrids cannot be explained in this way. Apparently the Lima race of *glutinosa* used in our hybrids is genetically distinct from the race used by McCray in respect to leaf characters.

In general, both the diploid and the amphidiploid hybrids are of a semi-arborescent type, and very vigorous. Of the parents, *tomentosa* is of this habit and, as was pointed out by Goodspeed (1933*a*, p. 311), while the commonly grown races of *glutinosa* are herbaceous annual plants, this new Lima race is more arborescent and tends to be perennial. He also draws attention to the fact (*loc. cit.,* p. 313) that F_1 *glutinosa* × *tomentosa* strikingly resembles the species *wigandioides* and mentions the possibility that the latter species originated from such a cross.

Of the diploid hybrids *N. glutinosa* × *tomentosa,* two individuals have been grown in the University of California Botanical Garden this summer (1933), one in the greenhouse and one in the field. In meiotic behavior these plants were equivalent and they are treated together in the following discussion.

The reduction division was studied in microsporogenesis. Two variations of the acetocarmine method were used: (1) the anthers were at once smeared in the acetocarmine solution on the slide; (2) the buds (after removal of sepals and petals) were first fixed in 7 parts absolute alcohol and 3 parts glacial acetic acid for *ca.* two hours. After transfer through 95 per cent and 90 per cent alcohol, they were stored in 80 per cent alcohol. As they were wanted, the anthers were crushed in acetocarmine.

By the latter method, a modification of McClintock's technique (1929), it was possible to get useful preparations of the pachytene stages. In this technique, the slides were gently heated and the coverglass lightly pressed in order to flatten the PMC and to obtain a spreading of the chromatin threads. For later stages also, more uniform and satisfactory results were obtained by the second procedure, omitting the heating and pressure. In order to eliminate the darkening of the cytoplasm at IM, which tends to follow such treatment, the following modification was used. When the PMC were properly stained, the saturated stain-solution was replaced by a dilute one, which was drawn under the coverglass with filter paper. For pachytene stages, this procedure was not necessary because of the thinness of the cytoplasmic layer, these pressed preparations lasting at least a month without serious darkening of the cytoplasm.

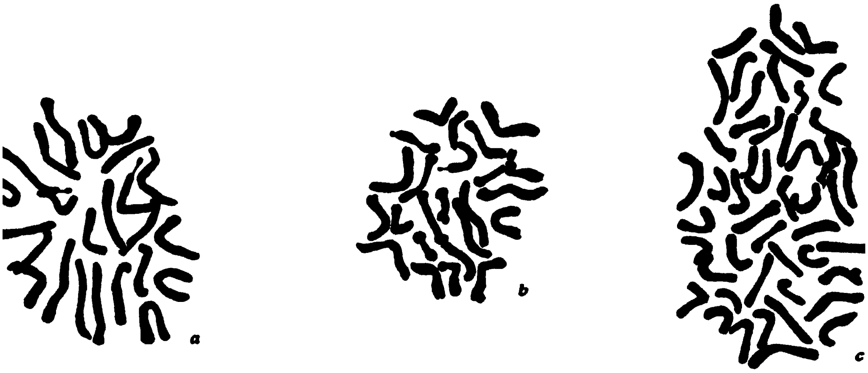

Fig. 1. Somatic metaphases. *a, Nicotiana glutinosa. b, N. glutinosa* × *tomentosa,* diploid. *c, N. glutinosa* × *tomentosa,* amphidiploid (no satellites visible in this plate).

Some studies were also made of the somatic chromosomes. Root tips were obtained from cuttings of the greenhouse plant of the diploid and of the amphidiploid hybrids. For purposes of comparison, root tip fixations were also made of *N. glutinosa.* Navashin's fluid was used and the staining was done with gentian-violet. Preliminary studies of the somatic chromosomes did not reveal anything of special interest, however, and they were therefore carried on only far enough to obtain a sufficient number of clear plates for determination of the chromosome number with certainty. One of five root tips examined from the diploid hybrid was tetraploid (cf. Ruttle, 1928, p. 219; Avery, 1929, p. 269; Kostoff, 1930, p. 64). Since it is known (Goodspeed, MS) that *tomentosa* has shorter chromosomes in its idiogram than *glutinosa,* it was hoped that it would be possible to distinguish the parental chromosome sets in the hybrid. A comparison of the somatic plates shown in figure 1 gives a slight but not convincing impression that there is a greater proportion of small chromosomes in the hybrids than in *glutinosa.*

THE MEIOTIC DIVISIONS

In studying the meiotic divisions, attention was confined almost exclusively to mid-pachytene and first meta-anaphase. Intermediate stages appear to be passed through very rapidly and were found only rarely (cf. Goodspeed and Clausen, 1927, p. 119). Also, with the technique used it was difficult to obtain good pictures of these intermediate stages. Thus in diplotene the chromosomes were still too much entangled to permit an analysis and in diakinesis it usually was impossible to distinguish between true bivalents and "off-spindle attachments" (Lammerts, MS). In the early metaphase all chromosomes were packed closely together and interpretation of the plates was difficult and uncertain.

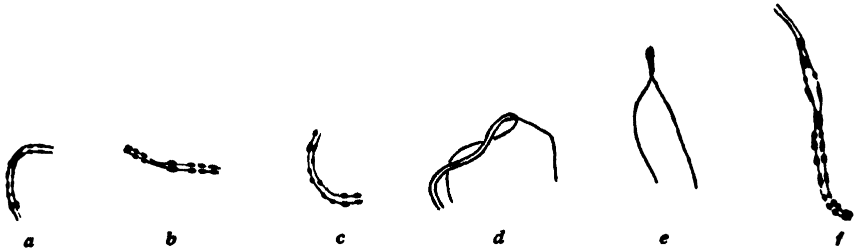

Fig. 2. Parts of the chromosomes at pachytene. *a-e, Nicotiana glutinosa* × *tomentosa*. *f, N. tomentosa.*

Pachytene.—In mid-pachytene both paired and unpaired threads occur, though the paired are much more numerous than the single threads. Variation in the degree of pairing from one PMC to the next was seen, but this might as well be the result of the difference in pairing in consecutive stages as the result of an actual unlikeness between the cells. Thus in many PMC scarcely any unpaired threads could be seen. Loops and free ends could often be studied in detail with respect to the chromomeres. The material was not ideal for such study, however, because of the large amount of chromatin and relatively small cells involved, so that only rarely was a sufficiently long section of a chromosome free from the general mass. Thinner spreading, which could be accomplished by additional pressure on the coverglass during preparation, only resulted in the chromosomes taking on an unnatural, stretched appearance, like that described as sometimes occurring in *Zea* (McClintock, 1931, p. 4 and fig. 25). A close examination of the double threads, where they are clear and well fixed, shows that sometimes (fig. 2*a, b*) the chromomeres obviously match each other and from their morphological appearance might be judged to be homologous. In other figures they obviously do not match (fig. 2*c*.). This cannot, however, be taken as a priori proof that the chromomeres involved are not homologous, since the chromomere differences between the threads may have arisen through improper fixation or by the threads being pushed away along each other, as a result of the squeezing of the cells during the preparation, in order to force homologous loci apart. In order to get evidence on this matter, the pachytene stage of *N. glutinosa* was studied (of *tomentosa* no material was available at the time of the investigation). As was expected, this species showed only paired threads with the chromomeres matching (fig. 2*f*). Only occasional, small differences occurred and they are most probably caused by fixation artifacts (cf. Belling, 1933, p. 409). Thus one may conclude that such unlikeness between the paired threads as occurs in the hybrid is an indication of lack of homology. The figures correspond closely to the non-homologous association described by McClintock (1932), Burnham (1932*b*), and Lammerts (MS). Special conditions, both of them seen several times, are shown in figure 2, *d* and *e*. In figure 2*d* the two threads are paired for a distance and then suddenly turn apart, indicating a possible change of homology. In figure 2*e* the terminal portions of two threads are associated but below this region the threads are free for as far as it was possible to follow them. "Backfolding" of univalent threads (McClintock, 1932, and Lammerts, MS) also occurs. Figures indicating reciprocal translocations or inversions as described in *Zea* by McClintock (1930, 1931), Cooper and Brink (1931), Brink and Cooper (1932), and Burnham (1932*a*, 1932*b*) were not identified, nor was there evidence that one chromosome would pair with more than one other chromosome in different parts of its length.

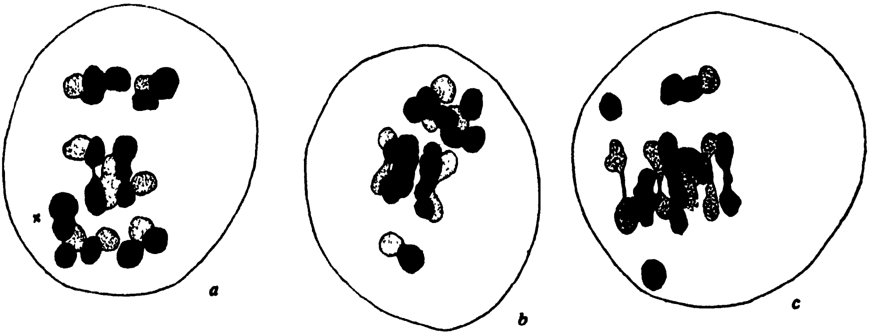

Fig. 3. *Nicotiana glutinosa* × *tomentosa*. Meta-anaphase. *a*, 3_{II} 18_{I} (at *x* an "off-spindle attachment"). *b*, 6_{II} 12_{I}. *c*, 8_{II} 8_{I}.

Meta-anaphase.—One of the most striking features observed in the hybrid at IM–A was the variability in number of bivalents. It became clear that the best way to study this variation was in side views of the early anaphase (fig. 3). Most of the univalents have at this stage passed to the poles, while the bivalents, and usually from one to four univalents, are lying in the equatorial zone. The size differences that are sometimes seen between the partners of a bivalent are too small to be significant. They are probably more apparent than real and may arise because the chromosomes are lying obliquely. The bivalents as a rule have the "loose" rod-shaped or dumbbell form which indicates, according to Darlington's theory (1930, p. 68), one-chiasma connection (fig. 4, *a-d*). Conditions like those shown in figure 4, *c* and *d*, indicate that the chiasma often is interstitial (cf. Darlington, 1931*a*, p. 419). For purposes of comparison, the usual form of the bivalents in the pure species, *glutinosa*, is shown in figure 4, *e-g*. Table 1 shows the variation in amount of pairing found in the hybrid. As the cells with a higher number of bivalents were more difficult to analyze, it is possible that in the selection of PMC, some favor was shown to those with lower bivalent numbers. The evidence in table 1, however, undoubtedly gives a true picture of the range of variation, namely, the main range from 3 to 8 or 9 with the mode at about 5 bivalents. This is true for both the greenhouse plant and the field plant and with either of the two methods of fixation. Some differences seemed to occur in the bivalent count from one slide to the next. This may represent a response to differences in external factors, but no attempt was made to obtain detailed evidence on this point.

TABLE 1

Nicotiana glutinosa × *tomentosa*
The variation in pairing in 100 PMC, IM

Number of bivalents	2	3	4	5	6	7	8	9
Number of cells	2	12	22	25	18	10	9	2

In addition to the regular bivalents in the equatorial zone, the approximation of two univalents to form an apparent "pair" outside the spindle was often observed (fig. 3*a*). This "off-spindle attachment" (Lammerts, MS) has not been taken into consideration in table 1 and presumably is merely an effect of fixation. Trivalent formation was seen only once (fig. 4*h*).

Later stages.—Nothing unusual in hybrid meiosis is found at IA and later stages. At IA lagging univalents are usually seen, probably those which were lying in the equatorial zone when the bivalents divided. They show the secondary split markedly, but actual division taking place rarely if at all. Most of them are finally included in the main nuclei, though often one is left out and then forms a micronucleus during interkinesis. An elongated, bent spindle is often noticed and thus pictures like figure 4, *i* and *j*, arise. The second division is regular, the two spindles showing a highly variable number of chromosomes, as would be expected following the irregular distribution of the chromosomes in the first division. In more than 50 per cent of the tetrads one or two small microcytes are seen, probably corresponding to the chromosome or chromosomes that were left out at the first division. Divisions leading to the formation of unreduced nuclei are very rare; a fusion of the two spindles in the second division was seen only once, and only once was a dyad found. The sterility of the hybrid is complete and in the pollen all or practically all the pollen grains are seen to be shrunken and aborted, as in the related hybrid *N. glutinosa* × *tomentosiformis* (Kostoff, 1932, p. 338).

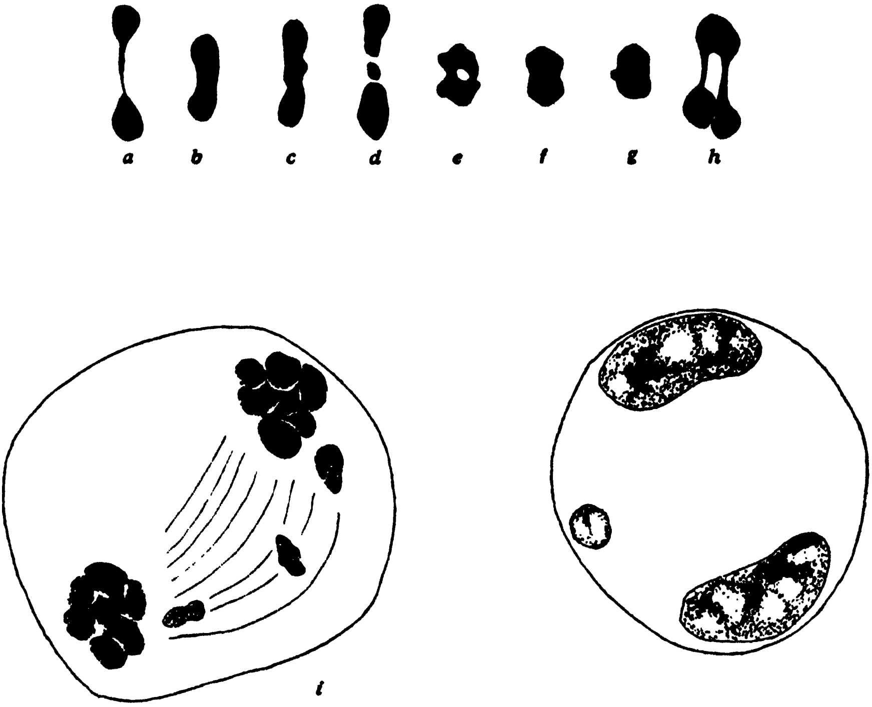

Fig. 4. *a-h*, Chromosome associations. *a-d*, *Nicotiana glutinosa* × *tomentosa*. Various types of bivalents. *a-c*, Meta-anaphase. *d*, Anaphase. *e-g*, *N. glutinosa*. Bivalents, metaphase. *h*, *N. glutinosa* × *tomentosa*. Trivalent.
i-j, *N. glutinosa* × *tomentosa*. *i*, Late anaphase. *j*, Interkinesis.

DISCUSSION

Although it was long ago pointed out by Strasburger (1905, p. 40) and A. and K. E. Schreiner (1906, p. 470) that the conjugation of homologous chromosomes in meiosis is not brought about by affinity between the chromosomes as a whole but rather by affinity between homologous chromatin units, the chromomeres, this distinction was not generally stressed by earlier workers. Such an interpretation of chromosome pairing is now being emphasized because it has been cytologically shown that rearrangements of chromomeres may occur both within a single chromosome and between different chromosomes (McClintock, 1930, 1931) and that in the meiosis of polyploids the chromomeres of one chromosome may pair, to a certain degree, independently of each other (Newton and Darlington, 1929, p. 12). According to the theory of Darlington (1929, *et. seq.*), association of chromosomes in pairs at later stages is a result of chiasma formation between the paired threads in prophase and this formation of chiasmas is approximately proportional to the length of the paired threads. This theory was put forward to explain the random and irregular formation of polyvalents in autopolyploids and the fact that in a number of species the shorter chromosomes were found to show irregularities in pairing in metaphase.

To interpret the meiotic behavior of a hybrid like F_1 *Nicotiana glutinosa* × *tomentosa* according to this theory, a certain structure of its chromosomes must be assumed. As shown above, this hybrid belongs to that class in which at IM a variable number of "loose" bivalents appear. It may be noted here that, in the amphidiploid, tetravalents are not formed at all or only in a small number not corresponding to the number of bivalents in the diploid. According to Darlington (see Darlington, 1931*b*, p. 238), this behavior is explained by assuming that the *glutinosa-* and *tomentosa*-chromosomes contain, in linear sequence, homologous and non-homologous parts. In the diploid hybrid two partly homologous chromosomes pair with their homologous segments, and this may result in the formation of one chiasma, giving in the metaphase a "loose" bivalent, or a chiasma may fail to be formed and the chromosomes appear in later stages as univalents. Only rarely more than one chiasma will be formed, resulting (in *Nicotiana*) in a normal-looking bivalent. Thus, the same randomness is seen in bivalent formation as is observed in polyvalent formation of polyploids. In the amphidiploid with two full sets of both *glutinosa* and *tomentosa,* each chromosome will have an identical partner and the small homologous segments of the different sets will rarely be able to effect a "competitive" pairing that will give tetravalents. Darlington (1931*a*, p. 469; cf. also Mather, 1933, p. 256) further assumed that each difference of homology would also interfere with the pairing of adjacent parts of the chromosome and thus still further suppress the possibilities of effective pairing, but this interpretation has been opposed by Brink and Cooper (1932, p. 446).

The significance of the pachytene evidence described above calls for comment. The *glutinosa* parent showed all threads paired with equivalent chromomeres matched, while in the hybrid a very large proportion of the threads also were paired at mid-pachytene, but although in some parts of the threads the chromomeres corresponded to one another, in other parts they were unlike and apparently not homologous. A similar higher degree of pairing in early pachytene than would correspond to the metaphase pairing seems also to occur in some *Lepidoptera* hybrids with variable pairing (Cretschmar, 1928; cf. Federley, 1914, p. 10). How much of this kind of association is the result of backfolding of univalent threads or non-homologous association among unlike threads, as in *Zea* (McClintock, 1932) or the haploid *Nicotiana tabacum* (Lammerts, MS), cannot be concluded decisively. It should, however, be remembered that there was often a complete pairing of all threads and this is most readily explained by assuming the conjugation of *glutinosa* and *tomentosa* threads, which are to some degree homologous. A complete pairing in early pachytene and incomplete formation of bivalents in later stages have been noted by Beadle (1932*a, b;* 1933) in asynaptic maize and in *Zea* × *Euchlaena* hybrids. A similar greater degree of pairing in prophase as compared with metaphase pairing seems also to occur in some *Lepidoptera* hybrids with variable pairing (Cretschmar, 1928; cf. Federley, 1914, p. 10). An analogous situation in *Taraxacum* and *Hieracium* is referred to by Rosenberg (1930, p. 51). It may be dangerous to attempt to draw conclusions from this evidence but it might be pointed out that such behavior would favor the view that chromosomes come together in the early pachytene through the affinity between a number of homologous loci (cf. Dobzhansky, 1931, p. 224; Lindstrom and Humphrey, 1933, p. 207), or even by a general affinity between the threads (cf. East, 1933, p. 286). Non-homologous segments would not become effectively conjugated and would therefore fall apart because there was no formation of chiasmas. (Cf. Beadle, 1932*a*, p. 493.)

Concerning the origin of the non-homologous parts of the chromosomes in the different genoms, it has been more or less emphasized by Cretschmar (1928, p. 365), Dobzhansky (1932, p. 277; 1933, p. 402), and Kihara and Lilienfeld (1932, pp. 388–89) that they arise, in part at least, through rearrangements such as inversions and translocations. The chromosomes involved would then have no complete homologues and through the conflict of the attracting forces a reduced pairing would occur. The observed formation of polyvalent chromosomes in hybrids, for example, in the *Lepidoptera* and in the *Triticum-Aegilops* circle, is in accordance with this view. For *Nicotiana glutinosa* × *tomentosa*, with only a sporadic trivalent observed in the metaphase, and the pachytene stage not clear enough to give certain information in this respect, this interpretation may be correct, but the evidence so far obtained indicates that the differences between the genoms of the parent species are to be attributed more largely to qualitative differences than to differences in arrangement of the same genic material. For the present, however, further discussion of these and related questions will be postponed. As mentioned above, this investigation will be continued, the behavior of the amphidiploid hybrid and its derivatives being the special subject of study.

The investigation here described was carried out at the University of California during the summer of 1933, while the author held a fellowship from the Swedish-American Foundation. I wish to acknowledge my gratitude to the Foundation for the grant of the fellowship. I am also indebted to Professor T. H. Goodspeed for the material used in this study, for the facilities provided, and for advice throughout the investigation; and to Professor R. E. Clausen, Dr. P. Avery, and Dr. W. E. Lammerts for helpful criticisms and suggestions.

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HARVEY M. HALL began his scientific development as a field naturalist in the vicinity of Riverside, California, having come with his parents and three brothers from Lee County, Illinois, where he was born on March 29, 1874. Stimulated and encouraged by the sympathetic interest of an understanding high school teacher, E. A. Zumbro, he and another youth (Edmund Heller, at present the director of the Milwaukee Zoölogical Garden) became collectors of birds' eggs. This led gradually to other fields of nature study and, before long, Hall made the acquaintance of Samuel B. Parish, a local botanist who was already well known to some of the most eminent plant systematists of America and Europe. By this time Hall was teaching school and was actively interested in the flora of the Riverside region. Hearing of Mr. Parish, he began sending him plants for identification. This led to visits back and forth and young Hall was soon a welcome visitor at that comfortable farm home where so many eminent botanists were entertained from time to time. How fortunate that in those early impressionable years the young man should have come under the influence of an older botanist of such open mind, good judgment, kindliness, and dignity! For there were native qualities in the youth which responded to such an atmosphere as a plant responds to sunshine. Prominent among those qualities were the two mentioned by his friend, Heller, after Hall's death, when he wrote: "The world needs today many more men of Harvey's absolute honesty and charming personality. I know only a few men of his equal in these respects."

In 1898 Hall entered the University of California, where he was graduated in 1901, having studied under Professors Setchell, Jepson, and Osterhout. A year later he received the degree of Master of Science, his thesis being A Botanical Survey of San Jacinto Mountain. Meanwhile he had published his first botanical contribution, the first of his "Studies on Californian Plants," in which four new species and varieties were described with that extreme care for detail in description and regard for system in citation of specimens which characterized all his published taxonomic work. In his master's thesis, the initial paper of the University of California Publications in Botany, he combined taxonomical, ecological, and distributional studies in such a way as to present a picture of the flowering plants of the region that will have an enduring value.

In 1906 Hall received the degree of Doctor of Philosophy at the University of California, his dissertation being a systematic treatise on the Compositae of Southern California. In reviewing this work Professor J. M. Coulter (1908) points out that:

> The 445 species and varieties are distributed over an area the size of Pennsylvania. This number would be largely increased if the author were not very conservative in his conception of species. The contribution is a manual of readily recognized forms which are further brought within easy reach by the numerous well-constructed keys. It is unusual to find in so extensive a contribution that only three new species are described. The reduction of numerous names to synonymy may be a service or may add to the confusion, dependent upon the care with which the types were studied.

Those who are familiar with Hall's methods in plant systematics will rest assured that the types were carefully studied whenever they were available and that, whether the types were available or not, all other possible contributory evidence was duly considered before reaching a conclusion.

Following several years of training as herbarium assistant and assistant in botany in the University of California, in 1902 Hall was placed in charge of the herbarium and in 1903 he became instructor in botany in charge of the botanic garden. In 1908 he was appointed assistant professor and in 1916 associate professor, which rank he held until he resigned from the University in 1919 in order to accept a position with the Carnegie Institution of Washington. His teaching in the University included undergraduate instruction in economic botany and graduate instruction in systematic botany. Throughout this period he served as curator of the herbarium (without official title) and to the work of organizing and increasing the collections he gave constant thought and ceaseless effort. While he was curator more than 190,000 mounted specimens were added to the herbarium, and all together he contributed at least 20,000 specimens of his own collecting, including duplicates which were used in exchange. He had a large share in bringing about the gift to the University of California of the Brandegee Library and Herbarium, valued at $30,000. During most of this period he also served as assistant botanist in the Agricultural Experiment Station, and in this capacity he fulfilled numerous duties such as the identification of weeds, economic plants, and exotic ornamentals, and various coöperative investigations with other members of the Experiment Station staff and the United States Department of Agriculture.

It was while he was connected with the University that Hall became keenly interested in botanical gardens and came to think of them as an important part of the working equipment of every botanical institution. So impressed was he with the need for such a garden at the University of California that he strove diligently for the recognition of this need and proposed the site occupied by the present botanical garden in Strawberry Cañon. Although the Board of Regents officially set aside this area for botanic garden development, yet no funds were made available during Hall's connection with the University. Not discouraged by that disappointment, however, Hall never abandoned the hope of seeing the beginning of a really great and richly endowed botanic garden and research institution somewhere in California. Meanwhile, after accepting appointment with the Carnegie Institution, his own needs for garden facilities were admirably met by the various transplant gardens which were provided at four different stations for his own investigations. The twelve years during which he was a member of the Carnegie Institution were his period of greatest productivity in published research.

The bibliography of Hall's published writings contains eighty-four entries. Although a number of them are progress reports published in the Year Book of the Carnegie Institution, yet aside from these there are far too many separate papers to permit a discussion of each of them in this brief sketch. Hall's productive career may be roughly divided into two main periods with an interlude representing the period of the World War.

In 1910 Hall married Carlotta Case, a former student in the University of California and a student of western ferns. With a common interest in systematic botany, Dr. and Mrs. Hall undertook the joint preparation of a flora of Yosemite National Park. This was a particularly happy choice since it took them frequently into that part of the Sierra Nevada which Hall most loved; it also afforded an opportunity to demonstrate the feasibility of presenting scientific plant classification in semipopular form. The degree of success attained is well indicated in the review by Nelson (1912) from which the following is an extract.

> Professor and Mrs. H. M. Hall are pioneers in the production of a local flora of one of our great natural playgrounds. This little manual is significant in many ways. In indicates an increasing interest in technically correct science simply and clearly expressed. It emphasizes the fact that systematic botany should be developed for the *use* of the people, not to impress them with the futility of trying to fathom the mysteries of recent nomenclatural practices. It shows that the breeze is beginning to blow steadily from the ocean, littered with the wreckage of families, genera and species, to the solid shores on which an *Astragalus* is an *Astragalus* and not a *Tium*, a *pine* is a *pine* and not an *apine.*

The Yosemite Flora is in some respects the high point of achievement in Hall's earlier period of productivity. In this period he also published several taxonomic contributions of a thoroughly critical kind, in addition to the Survey of San Jacinto Mountain and Compositae of Southern California. In one of them he first called attention to the lamentable confusion arising from the all too frequent practice of naming ecologic forms as new species.

During the period of the World War Hall gave considerable attention to two matters of great public interest. One of these was the investigation of plant pollens as the specific cause of hay fever. In coöperation with Dr. Grant Selfridge of San Francisco and, later, with representatives of the American Society for the Prevention of Hay Fever, he carried on the botanical studies which led to the publication of a report on certain groups of plants of importance in the Rocky Mountain States and a list of the important hay-fever plants in the Pacific Coast States. Here again the problem of species-concepts came to the fore and assumed a very practical aspect.

The other subject of public interest, especially during the war period, was the problem of an emergency supply of rubber in the United States. Recalling an earlier observation that the Indians of Inyo County obtained a gum by chewing certain kinds of Rabbit-brush (*Chrysothamnus*), Dr. Hall and Dr. T. H. Goodspeed investigated many specimens of this and other genera of desert plants and found at least one species that represents a potential supply of commercial rubber of high grade. As an outgrowth of this work Dr. Hall and Dr. Frances L. Long examined for rubber content about 225 species of herbs and shrubs, many of them being milkweeds (*Asclepias*). About six shrubs and sixteen perennial herbs were considered worth studying further while one species of *Asclepias* seems to be of marked promise not only as a source of rubber but also of fiber and paper pulp. On July 1, 1923, Dr. Hall was appointed collaborator in rubber investigations in the Bureau of Plant Industry, United States Department of Agriculture, and continued in that capacity until his death.

During the war period Hall also found time to summarize his various distributional studies involving the recognition and definition of life zones characteristic of montane floras. In collaboration with Dr. Joseph Grinnell, he published in 1919 a paper on Life-Zone Indicators in California in which are given lists of plants and animals which may serve as guides in working out the life zones of unmapped areas.

Hall's primary scientific interest was the taxonomy of flowering plants, especially the Compositae. After he was officially connected with the Carnegie Institution he continued to reside in Berkeley until the establishment of the Division of Plant Biology of the Carnegie Institution at Stanford University in 1929. From the beginning of this period until his death he held the position of honorary curator of the herbarium in the University of California. In 1929 Hall was appointed acting professor of botany in Stanford University. Throughout the later period of his career he continued the study of his extensive collections* of western American Compositae and published monographs on four large genera.

Three of these monographs were published in 1923 in collaboration with Dr. F. E. Clements. As was stated by Coulter (1926), this contribution suggests some fundamental changes in the preparation of taxonomic monographs. Examination of the introduction reveals the broad philosophic outlook which inspired the monographer. The following brief quotations indicate the point of view held by the authors;

> If it [taxonomy] is to reflect evolution as accurately as it should, it must regard physiological adjustment as the basic process, and morphological and histological adaptations as the measurable results. This means that the taxonomist of the future will think in terms of evolutionary processes, and will learn to treat his morphological criteria as dynamic rather than static.
>
> In short, experimental and quantitative methods promise to turn taxonomy from a field overgrown with personal opinions to one in which scientific proof is supreme. Such a taxonomy is indispensable to the advance of ecology, and apparently can be attained only by adopting its methods

It was because of his appreciation of the potential service of genetics in throwing light on evolutionary relationship that Hall invited the writer to collaborate with him in the intensive study of a group of "species" known as the Hay-field Tarweeds. A joint paper was published presenting a synthetic view of the evidence from genetics, ecology, and comparative morphology of this group of forms and the resulting taxonomic treatment. Here, as in his earlier monographs, Hall recognized the subspecies as the only intraspecific category worthy of receiving a Latin name and catalogued the variants of lesser rank in a serial list. He defended this procedure on the grounds that it tends to simplify botanical nomenclature, a simplification which is sadly needed; and that, if used consistently, it aids in applying the phylogenetic method in plant taxonomy.

The same principles of classification were observed in the preparation of his last monograph, on the genus *Haplopappus*. But the methods used in investigating this genus were limited to field and herbarium studies with some assistance from the transplant experiments in which plants of the section *Pyrrocoma* were used. Otherwise the detailed ecologic and genetic experiments employed in his earlier monographic work had to be dispensed with on account of lack of time. Hall's experience in undertakings of this sort, however, provided a sound basis on which to work and it is very probable that future students of this genus will find that in this work the author's main objectives were attained with a high degree of accuracy with respect both to phylogenetic position of the genus and to intrageneric relationships.

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* Hall's botanical journeys covered a period of thirty-seven years (1895–1931). A fairly accurate record of these collecting trips has been prepared with the assistance of Mrs. Carlotta C. Hall. This record has been mimeographed and is available for distribution by the Carnegie Institution of Washington, Institute of Plant Biology at Stanford University, California.

It should be noted that another extensive monographic project in the Compositae was already well advanced before Hall's death. This work began with the genus *Hemizonia* and was gradually extended to cover several genera in the endemic subtribe *Madinae*. Extensive collections, field studies, transplant work, and genetic experiments had been carried out; and some parts of the manuscript were finished. It is gratifying to know that the importance of this work has been recognized by the Carnegie Institution and that provision has been made for its continuation and for completing the monograph.

In his latter years, Hall became more and more interested in the international aspects of plant taxonomy. This interest was a natural outgrowth of his monographic studies and was increased by two trips abroad during which he made numerous professional contacts and established friendly relations in a number of important botanical centers. His chief work while making these visits was herbarium research, but his interests were numerous and broad, ranging from such problems as moot points in botanical nomenclature to the scientific and social aspects of national parks.

Nomenclatural difficulties were continually arising in his work. While he always maintained an independent attitude, somewhat like that of his first botanical friend and teacher, S. B. Parish, yet he was sincerely desirous of conserving the best practice with respect to general usability. To this end he supported and followed as fully as possible the International Code of Nomenclature; and it was for this reason that he proposed *Laya* as an addition to the list of *nomina generica conservanda* in 1926. This proposal was made after much careful study and with the advice and approval of Dr. John Briquet, for whose knowledge and judgment in this difficult field Hall had the greatest respect.

One result of Hall's first European trip is of special significance in the history of botanical taxonomy, while it also reveals Hall's breadth of interest in and unselfish devotion to this branch of botany. One of the herbaria in which we both had worked in that year abroad was the Muséum d'Histoire Naturelle in Paris. We were so impressed by the deplorably inadequate conditions which then existed in that herbarium that we had several conferences over the matter on the return voyage. Before landing in New York, we prepared a letter and sent it to the office of the International Education Board in Paris, urging an investigation and financial assistance from the Rockefeller Foundation. Eventually an understanding was reached between the Foundation and the French Government, and in accordance with this a grant was made by the

Foundation contingent upon the appropriation of a like amount by the French Government for the construction of a new building at the Muséum d'Histoire Naturelle to be used for herbarium purposes. When at last construction of the new building was assured, Hall was invited by Professor H. Lecomte, Director of the Laboratories and Muséum, to prepare a report upon herbarium construction and technique for the guidance of the Muséum in planning the new building. Hall gave himself up sympathetically to the preparation of this report, which covered ten closely typewritten pages under the following principal topics: the building; rooms and their arrangement; herbarium cases and their arrangement (based mainly on data supplied by Dr. B. L. Robinson); methods of filing specimens; central bureau of taxonomic research. This report was translated into French and was accompanied by a plan, photographs of American herbaria and equipment, and a detailed proposal for photographic rooms, this last having been prepared by Dr. Carl Epling.

It was with the same deep appreciation of the importance of international unity in science that Hall assisted in a similar though a more modest attempt to save the Conservatoire et Jardin Botanique of Geneva, Switzerland, from serious financial embarrassment. This well-known conservatory contains the famous De Candolle Herbarium and Library as well as other collections of world-wide importance. As director, the late Dr. John Briquet was compelled to appeal to the botanists of the world for support in providing proper maintenance for those invaluable collections. Fortunately for plant systematics, the response was not only sufficient to refill the then vacant herbarium assistantships but also to construct an additional wing to the conservatory building.

Another product of Hall's cosmopolitan interests in taxonomy, and one of even greater potential value than new buildings or aid in maintaining herbaria, was his proposal for an international bureau of plant taxonomy. This plan was presented in the form of a short paper in the section on Taxonomy and Nomenclature of the Fifth International Botanical Congress at the University of Cambridge, in 1930. Unfortunately, no action was taken on the proposals made in this communication. Nevertheless, they embody such valuable suggestions for the general progress of plant taxonomy that sooner or later they will doubtless be realized, at least in some degree.

Hall's most noteworthy contribution to biology is the influence which he has exerted and will continue to exert on the development of plant taxonomy on a more thoroughly scientific basis. From first to last this was his aim, and his series of monographs will serve as a lasting monument to his untiring efforts. Two aspects of his work should be emphasized, namely, experimental taxonomy, and synthetic coöperative research. It is a far cry from the attitude of the older school of taxonomy, in which a garden plant seemed hardly worthy of consideration as evidence on classification, to the attitude of experimental taxonomy which demands controlled cultures as an indispensable adjunct to herbarium and field studies. Hall's contributions to the advancement of the science of plant taxonomy are well summarized in his report on Experimental Taxonomy in Year Book No. 30 of the Carnegie Institution of Washington (1931) and in his posthumous paper on Heredity and Environment—as Illustrated by Transplant Studies (1932). In the former he and two of his associates discuss the composition of species; the evolutionary significance of "small species"; the differentiation between effects of heredity and environment by experimental methods; limits of modification of an organism; cytology and pollen morphology as aids to classification; and the results as applied to classification. The latter paper is based on the lecture which Hall prepared for the annual meeting of the Carnegie Institution at Washington in December, 1931, but which his final illness prevented him from delivering. It is an excellent summary of Hall's development of transplant experiments as an empirical method in taxonomic research and it indicates clearly the broad biological significance of these investigations.

The spectacular development of genetics and cytology as twin phases of biology during the first two decades of this century made a deep impression on Hall's mind. He appreciated their potential value as aids in taxonomy, and eventually he tried the experiment in coöperative genetic and taxonomic research on the Hay-field Tarweeds. Encouraged by the outcome of this trial he gradually matured his plan for associating himself with a group of experimental taxonomists. It was his ideal to work with men of demonstrated ability and absolute loyalty to the aim of true coöperation in the interest of synthesis and application of results. This aim was twofold: first, to place taxonomy on a truly scientific basis; second, to throw new light on the processes of organic evolution. It is fortunate that he was able so to develop this plan that about a year before his death there was added to the small group associated with him a man who had already shown ability in cytogenetic and taxonomic research, Dr. Jens Clausen, of Copenhagen.

The contributions of Harvey M. Hall to human welfare are many and various. They extend from the realm of personal influence throughout the range of his scientific and other professional activities. There is a circle of contemporary and younger biologists, as well as a larger group of his former students and friends, who cherish the memory of Hall's stimulating personality. While some of his scientific work was of direct application to human welfare, more important, without doubt, are his contributions to the advancement of plant science. Development of plant taxonomy on an increasingly sound basis and always toward the goal of usefulness to man, has been stimulated and aided by his efforts. His research had the ultimate goal of advancing man's knowledge of evolutionary processes in order that this knowledge might be applied for man's benefit. But equally worthy of acknowledgment are those dreams of his which are yet to be realized. Hall's faith in humanity was deep. He believed the necessary leaders would appear in due time to help make these dreams reality. Accordingly, he made plans in a broad way, with an eye to the far future.

At the time of the World War Hall outlined plans for botanical surveys and research that were merged later with a larger scheme which gradually developed as his vision of a great and richly endowed botanical institution. Already, in 1911, when he wrote to President Wheeler about the proposed garden in Strawberry Cañon, he was thinking in broader terms than a garden, for he dwelt on

> the importance of looking forward to a time when a botanical garden operated in connection with botanical laboratories, libraries and herbaria, where far-reaching studies in plant genetics, systematic botany, dendrology, plant pathology and physiology may be pursued.

Again, at a conference in 1917, he said:

> It is appropriate that a comprehensive botanical institute should be established in California. Our practical people are concerned with the growing of plants and the reaping of wealth and comfort from their products. Our home makers are interested in ornamental planting and landscape effects. The citizens of the state are progressive and they appreciate the importance of scientific investigations. A botanical institute established on broad lines would minister to all of these interests.

After the war Hall became the leader of a considerable group, mostly botanists, who, interested and fired by his imagination, made a beginning toward the working out of the great plan, which included not only California but the whole "Pacific Area" in its field of operations.

Of all the far-sighted projects that Hall completed perhaps the most significant is the establishment of a natural reservation, an area permanently set aside for the preservation of wild life, both plant and animal, under strictly natural conditions. Two principal aims guided his efforts in this direction. First, he wished to provide for future scientists a reservation which should be absolutely unspoiled. For a third of a century he watched with growing concern man's encroachment upon the most remote and beautiful retreats in our highest mountains. He concluded that some small part must be preserved and kept available for future research. His second aim was to provide, if possible, for use by the general public, some parts of such an area for purposes of recreation in the highest sense of the word.

With these problems in mind Hall took counsel with President Merriam of the Carnegie Institution of Washington and was authorized to make a survey of national parks and similar reservations in several European countries. This was done on a trip abroad in 1929. His report of this survey in the October, 1929, number of the Journal of Forestry is a source of much valuable information for both scientists and governmental agencies.

Hall concluded that there was urgent need in America for complete reserves, the exact uses of which would be determined by future needs. They would be scientifically studied but not disturbed. They might also serve the general public under certain restrictions. The fundamental purpose is preservation of natural conditions, and the best locations for such reserves would be within national parks and national forests, since the surrounding parts of those areas would serve as buffer zones of partial protection.

It was for the establishment of reserves of this type that Hall strove to create a precedent in the United States, and the two natural areas which he was instrumental in setting up were sufficient to serve that purpose. Through the good offices of the late Stephen T. Mather, first director of the National Park Service, a part of the higher region of Yosemite National Park, known as the White Mountain area, has been recognized as a permanent natural reserve. Hall also proposed, with the approval and support of President Merriam, that another natural area should be established outside of and adjacent to Yosemite National Park. Accordingly through the coöperation of the United States Forest Service and the Carnegie Institution of Washington an extensive tract of high country in the Mono National Forest but much of it above timber line, adjoining Yosemite National Park on the northeast and lying on the eastern slope of the Sierra Nevada between Tioga Pass and Mount Conness, has been set aside as a region "where natural conditions will be virtually free from disturbances excepting those necessary in the prosecution of scientific research. . . ." This reservation has been most appropriately named The Harvey Monroe Hall Natural Area.

An equally fitting tribute to this far-seeing student and leader in plant biology has been expressed by President Merriam in the official announcement of Hall's death:

> The scientific work of Dr. Hall was of a pioneer character, and made notable contribution to the taxonomic study of difficult groups in the flora of western America. Experimental work with plantings, conducted in different localities at which both hereditary and environmental effects could be investigated carefully, was used as the basis of a new classification, and as a fresh approach to the problem of organic evolution. With unstinted energy and exceptional devotion to scientific pursuits, Dr. Hall coupled an extraordinary technique through which results having great influence on future studies in botanical science are certain to come. After having crossed the continent for the purpose of delivering a Carnegie Institution lecture summarizing his latest conclusions and methods, he passed away on March 11, 1932, in Washington.

Appropriate memorials, other than his published writings and the natural area named for him, exist in the genus *Halliophytum* of the Euphorbiaceae and in the species named for him in several genera of California plants.

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NICOTIANA PHYLESIS IN THE LIGHT OF CHROMOSOME NUMBER, MORPHOLOGY, AND BEHAVIOR

BY

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In a previous discussion (Goodspeed, 1933) the chromosome numbers of forty investigated species of *Nicotiana* were listed and some suggestions made in respect to species origins and relationships. Among thirty-two species characteristic of the Americas, the monoploid numbers 9, 10, 12, and 24 occur, while Australasian species possess 16, 20, 22, and 24 pairs of chromosomes. Certain of the American species fall into "genetic groups" (Goodspeed, *loc. cit.*) which usually exhibit a characteristic chromosome number. The 24-paired American species are, probably, all of amphidiploid origin. The Australasian species make up a rather unified morphological group, possibly recent in origin and giving evidence of active differentiation. In the present communication will be given a summary and discussion of new data which indicate the extent to which studies of chromosome morphology and meiotic behavior give evidence of phylesis in the genus *Nicotiana.*

THE KARYOTYPES OF TWENTY-FIVE NICOTIANA SPECIES

Investigation of chromosome behavior in *Nicotiana* species and hybrids requires information concerning the karyotypes of the genus. Such information has been secured (fig. 1) but has itself pointed to the necessity of more detailed study of certain particulars of chromosome morphology. General characteristics distinguishing *Nicotiana* karyotypes are dealt with in table 1, where average length of the different genoms and the position of the spindle-fiber insertion region in the different members of a genom are included.

The genoms of the 12-paired species in table 1 are arranged in order of decreasing size. The size range throughout is not great and other distinctions in morphology are limited also. Nevertheless, no two species, except possibly *longiflora* and *plumbaginifolia,* possess genoms with chromosomes identical in form. Indeed the data submitted in table 1 emphasize the similarities, whereas a more detailed classification would direct attention to distinctions between the chromosome complements. The ALATA-GROUP (fig. 1*p-r*), more fully analyzed in table 2, illustrates this point.

For the species listed, chromosomes with median (M) or submedian (SM) insertion regions predominate, there being a total of 144 M or SM to 83 ST (subterminal). It is perhaps significant that 42 of the 83 ST pairs occur in four species, while the remaining 41 ST are distributed among eleven species. Five additional species have no ST chromosomes, their complements being composed of M or SM chromosomes. Whether a genom consisting entirely of chromosomes of one morphological type represents a more advanced condition than one containing chromosomes of diverse morphological types, cannot be determined from the evidence in hand. However, since the insertion region plays an important rôle in the mechanics of both mitosis and meiosis, it is conceivable that a uniformity in its position in the chromosomes of a complement might have selective value. There is at least a suggestion that this is true in *Nicotiana,* since the four species possessing all or predominantly ST chromosomes belong to three distinct genetic groups and presumably, therefore, evolved this type of genom independently of one another.

TABLE 1

KARYOTYPES OF 9_{II}, 10_{II}, AND 12_{II} SPECIES OF NICOTIANA

	Figure 1	Chms. length*	M or SM†	SM$_s$	ST	ST$_s$
12_{II} species						
glauca	a	4.5–5.5	2	....	9	1
Raimondii	b	....	11	1	....	....
solanifolia	c	4.5–5.5	11	1	....	....
undulata	d	....	11	1	....	....
acuminata	....	....	9	....	2	1
sylvestris	e	4.5	9	....	2	1
wigandioides	....	4.5	8	....	3	1
glutinosa	f	3.5–4.5	11	1	....	....
tomentosiformis	g	....	8	1	3	....
attenuata	h	....	7	1	3	1
Miersii	i	....	7	1	3	1
paniculata	j	....	11	1	....	....
Cavanillesii	k	....	....	....	10	2
tomentosa	l	2.2–3.2	6	1	5	....
trigonophylla	m	2.2	9	....	2	1
10_{II} species						
plumbaginifolia	n	2.2	....	....	10	....
longiflora	o	3.5	....	....	10	....
9_{II} species						
alata	p	3.5–6.6	5	....	2	2
bonariensis	q	....	5	....	2	2
Langsdorffii	r	....	5	....	2	2
Totals			135	9	68	15

* Average length in μ is given where chromosome (chms.) length varies little; elsewhere, range from shortest to longest is given.

† M = insertion region median; SM = insertion region submedian; SM$_s$ = insertion region submedian, proximal satellite; ST = insertion region subterminal; ST$_s$ = insertion region subterminal, proximal satellite.

All the species in table 1, except *longiflora* and *plumbaginifolia,* have at least one pair of chromosomes bearing proximal satellites. In six species there are two such pairs of chromosomes. In several species a satellited pair has been found to be associated with the nucleolus at late diplotene or diakinesis, but the relation of the two satellited pairs to the nucleolus in certain 9- and 12-paired species demands further investigation along the lines pursued by Heitz (1931). Also the origin of the nucleolus in *longiflora,* which Hollingshead (1929) showed to possess no typical satellited pair, should be of interest in this connection since a pair of chromosomes has been observed to be associated with the nucleolus at diplotene and diakinesis in this species just as in the species possessing satellited chromosomes. In *longiflora* (fig. 1*o*) and *plumbaginifolia* (fig. 1*n*), and in *Cavanillesii* (fig. 1*k*), and several of the Australasian species, distinct distal constrictions occur in certain chromosomes and these constrictions are often so pronounced that they give the chromosome the appearance of bearing a distal satellite.

Among the 12-paired species possessing predominantly chromosomes with median or submedian insertion regions, the karyotype pattern 9M or SM : 2ST : 1ST$_s$ appears to be the basic one. This formula is not characteristic of any one genetic group but appears in several different groups. The genetic group exhibiting greatest uniformity in genom formula is the PANICULATA-GROUP* including *paniculata* (fig. 1*j*), *solanifolia* (fig. 1*c*), *Raimondii* (fig. 1*b*), *undulata* (fig. 1*d*), and *glauca* (fig. 1*a*). Within this group *solanifolia, undulata,* and *Raimondii* have virtually identical genoms and *paniculata* is closely similar except that its complement is slightly reduced in size and possesses some further distinctions. As already noted, the genom of *glauca* sets it apart from the other members of its genetic group; indeed, the large size and predominantly subterminal insertion region of the chromosomes of this species mark it as outstanding in the genus in respect to chromosome morphology.

A second genetic group which is characterized by a distinct karyotype pattern is the ALATA-GROUP. As previously defined, it includes *alata, bonariensis, Langsdorffii, Sanderae, longiflora,* and *plumbaginifolia.* The first four of these species are all 9-paired and their karyotypes are similar as far as general details are concerned, with the pattern 5M or SM :2ST :2ST$_s$. The somatic complements of three of these species, on the contrary, are sharply differentiated in respect to the morphology of particular chromosome pairs. Thus in *bonariensis* (fig. 1*q*) one of the two large V-shaped chromosomes (M) in the monoploid set of *alata* (fig. 1*p*) is replaced by a large chromosome (SM) with a distinctly submedian insertion region, making it J-shaped. In *Langsdorffii* (fig. 1*r*) the size and shape of the chromosomes, in general, correspond to *alata* and

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* In a previous communication (Goodspeed, 1933) this group was once erroneously designated as the "GLAUCA-GROUP."

bonariensis. However, in place of the two similar pairs of satellited chromosomes found in the latter two species, there is one pair with extremely large satellites and another very small pair with small satellites. The former is peculiar to the *Langsdorffii* genom and suggests a similar satellite type found in *Crepis setosa* (Hollingshead and Babcock, 1930). The *Langsdorffii* pair possessing small satellites is shorter than any other chromosome pair in any of the 9-paired *Nicotiana* species. While one of the large chromosome pairs has a submedian rather than a strictly median insertion region, it is nevertheless closer to the V-shaped pair in *alata* than to the J-shaped pair in *bonariensis*. Further, a pair of *Langsdorffii* chromosomes with subterminal insertion region approximates in size and shape the satellited pairs in *alata* and *bonariensis* and characteristically shows a satellite-like body close to the chromosome "head" but never separated from it by a thread. These specific distinctions between the three complements, which in general morphological details are so similar, serve to set them apart from one another very definitely. It is to be noted that such distinctions could be accounted for by a few rather simple transformations, a suggestion which is supported by the evidence of meiotic behavior in F_1 hybrids between them.

TABLE 2

DETAILED ANALYSIS OF KARYOTYPES OF 9_{II} SPECIES OF NICOTIANA

	M*	m†	SM	ST	st	STs	ST$_s$	st$_s$
alata	2	3	....	1	1	....	2	....
bonariensis	1	3	1	1	1	....	2	....
Langsdorffii	1	3	1	2	....	1	....	1

* For notation see footnote †, table 1; large chromosomes are capitalized, small chromosomes are indicated by small letters; size of satellites, similarly.

† Some pairs included here probably are sm.

Just as *glauca* is distinct in chromosome morphology from other members of the genetic group in which it might be most natural to include it on the basis of external morphology, so *longiflora* (fig. 1*o*) and the closely related *plumbaginifolia* (fig. 1*n*) are set apart from the ALATA-GROUP, in which, on similar grounds, they have been placed. These two species differ from each other in average chromosome size and are distinct from the other species of the group by reason of the uniform occurrence of subterminal insertion regions. It is moreover to be remembered that these are the only 10-paired species in the genus.

The TOMENTOSA-GROUP consists of *tomentosa* (fig. 1*l*), *tomentosiformis* (fig. 1*g*), *glutinosa* (fig. 1*f*), and *wigandioides*. Distinctions in specific details of chromosome morphology distinguish all four species, while of special significance is the distinction between the genoms of

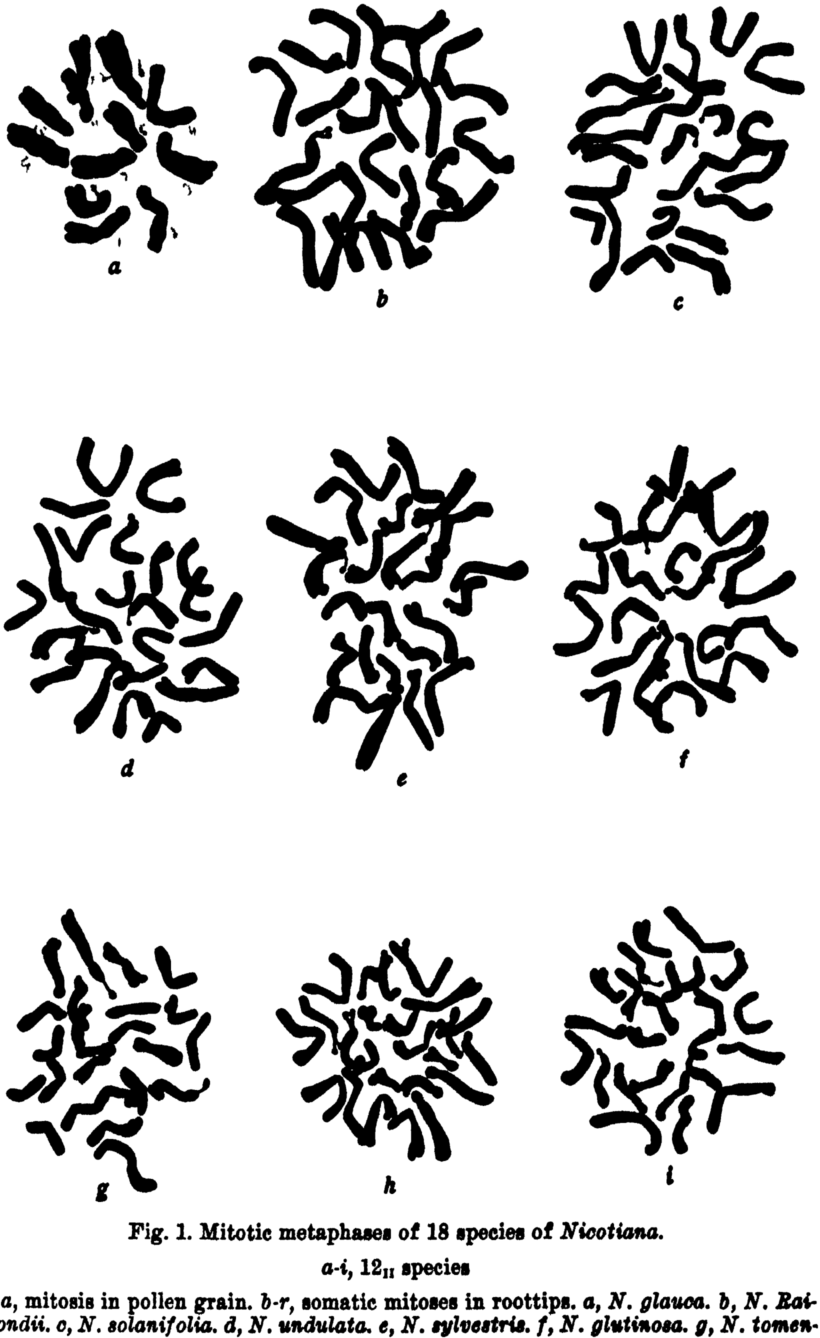

Fig. 1. Mitotic metaphases of 18 species of *Nicotiana*.

a-i, 12_{II} species

a, mitosis in pollen grain. *b-r*, somatic mitoses in roottips. *a*, *N. glauca*. *b*, *N. Raimondii*. *c*, *N. solanifolia*. *d*, *N. undulata*. *e*, *N. sylvestris*. *f*, *N. glutinosa*. *g*, *N. tomentosiformis*. *h*, *N. attenuata*. *i*, *N. Miersii*.

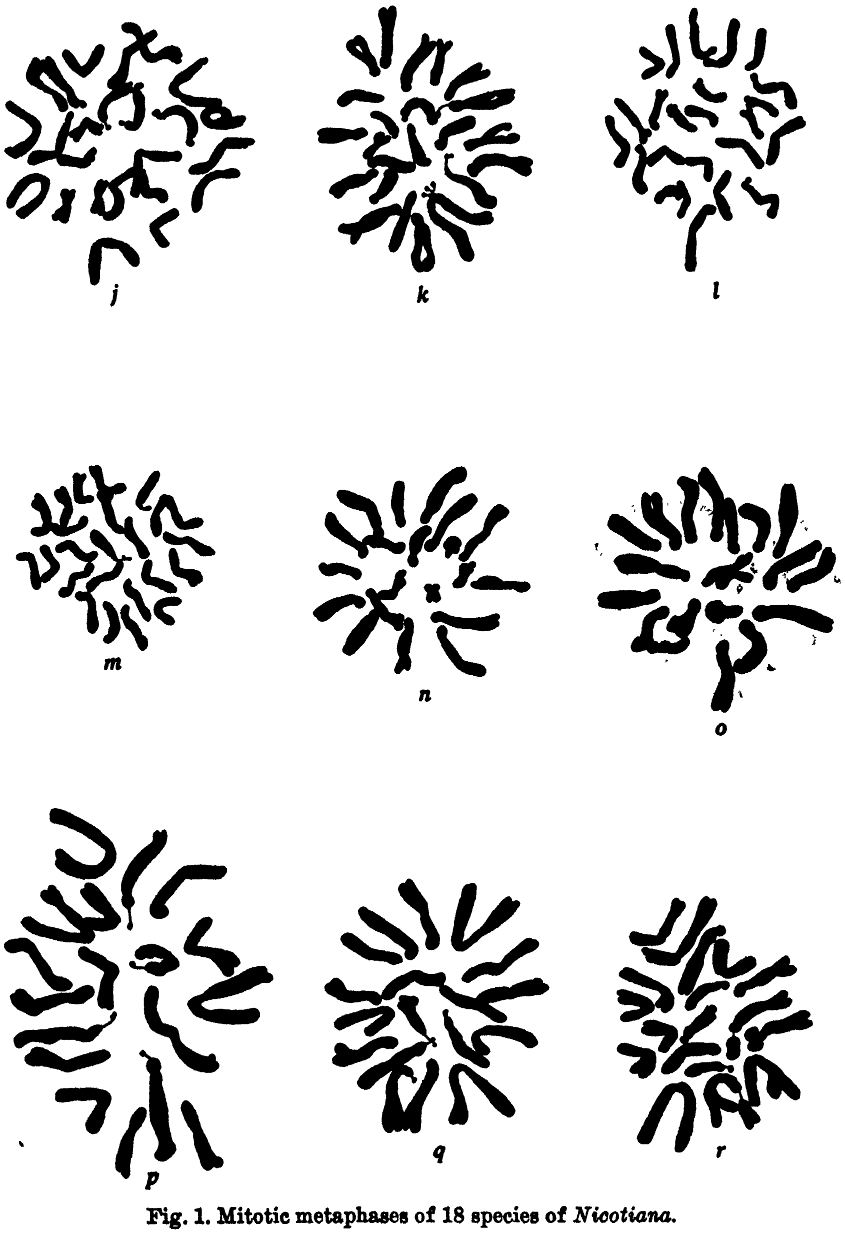

Fig. 1. Mitotic metaphases of 18 species of *Nicotiana.*

j-m, 12_{II} species. *n-r*, ALATA-GROUP

j, *N. paniculata. k*, *N. Cavanillesii. l*, *N. tomentosa. m*, *N. trigonophylla. n*, *N. plumbaginifolia. o*, *N. longiflora. p*, *N. alata. q*, *N. bonariensis. r*, *N. Langsdorffii.*

tomentosa and *tomentosiformis*, species which are closely related genetically. Thus, the latter has a complement of larger size than the former and in particular is characterized by two pairs longer than any pairs in *tomentosa.*

The REPANDA-GROUP consists of three species: *repanda, Stocktoni,* and its close relative *nesophila.* These are similar in basic features of external morphology and all possess 24 pairs. No information at present available confirms the obvious suggestion that 12-paired species have given rise to this group through amphidiploidy. It seems probable, however, that the three species represent segregation products from an original amphidiploid stock rather than three different amphidiploid species. They would be, therefore, equivalent to the distinct varieties of *Tabacum* or *rustica,* their geographic isolation rather than distinctions in origin and genetic relationships giving them specific rank. This interpretation is borne out by the genetic results obtained in crosses between *Stocktoni* and *repanda.* Thus the dark purple color on stems and corolla tubes of *repanda,* which is absent in *Stocktoni,* behaves as a Mendelian dominant in hybrids between the two species, as shown in table 3. Such close agreement to expectation for a Mendelian factor as is shown in this table indicates that the chromosomes of the two species must be very similar genically and structurally, and our observations of normal bivalent formation in the F_1 and its high degree of fertility (cf. Johnston, 1931, p. 95) confirm this opinion.

TABLE 3

SEGREGATION FOR COLOR IN N. STOCKTONI × REPANDA

		Colored	Uncolored
31.034	F_1 selfed	22	3
31.035	F_1 selfed	19	6
	Total	41	9
31.036	F_1 × repanda	25	....
31.037	repanda × F_1	25	....
	Total	50	....
31.038	F_1 × Stocktoni	15	10
31.039	Stocktoni × F_1	11	14
	Total	26	24

Cytogenetic evidence in respect to species origins and relationships within the SUAVEOLENS-GROUP will be discussed by Dr. H-M. Wheeler as a supplement to the taxonomic revision of the Australasian species of

Nicotiana which she has prepared. *N. suaveolens* and *maritima** are 16-paired species with complements consisting almost exclusively of chromosomes with median and submedian insertion regions. *N. Goodspeedii** is a 20-paired species, *rotundifolia* a 22-paired species, and *Debneyi* a 24-paired species, all with complements possessing a considerable number of chromosomes with subterminal as well as some with median insertion region and each having a satellited pair. Thus the karyotypes of these Australasian species are not directly comparable with those of any of the American species investigated, yet are not strikingly dissimilar (cf. F_1 *Bigelovii* var. *multivalvis* × *suaveolens,* table 5, C; and F_1 *Debneyi* × *nudicaulis,* table 5, D).

In addition to the above-mentioned species, table 1 includes six other species, only two of which, *acuminata* and *attenuata,* have provisionally been placed in the same genetic group (Goodspeed, *loc. cit.*). The genom of *trigonophylla* (fig. 1*m*) is chiefly noteworthy for the relatively small size of its chromosomes. They possess principally median or submedian insertion regions and correspond in size and shape more closely to those of *nudicaulis* than to those of any other 12-paired species, and this fact may in itself be an evidence of the relationship to be pointed out later (p. 395). Reference has already been made to *Cavanillesii* (fig.1*k*), with its small subterminally constricted chromosomes and its two satellited pairs. Its somatic complement is quite distinct from that of any other 12-paired *Nicotiana* species listed in table 1. Although *attenuata* (fig. 1*h*) and *Miersii* (fig. 1*i*) have been placed in different genetic groups, a preliminary analysis of their chromosome complements shows such a degree of similarity in size and shape that one would be inclined, on the basis of such evidence as that in table 1, to suggest a possible relationship here. Certain morphological features substantiate such a suggestion but until more evidence, especially from hybrids, is available it must remain a tentative one. It is also to be noted that the chromosomes of *attenuata* are in general size and shape close to those of *Bigelovii,* a 24-paired species, and as will be pointed out in what follows, other cytological evidence bears out the suggestion of relationship between the two species.

In respect to taxonomy, *sylvestris* occupies a rather isolated position. It is therefore of some interest to find that a variety of *acuminata* possesses a somatic complement very similar in size and morphology to that of *sylvestris* (fig. 1*e*). In fact its karyotype is not so distinct as are those of less taxonomically isolated species, such as *glauca* and *longiflora.* Whether this represents chance parallel variation in the evolution of two somatic complements or whether there is some causal relationship not yet appreciated, must await further evidence.

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* New species being described by Dr. Wheeler.

In general it may be said that the karyotypes of the *Nicotiana* species thus far investigated furnish little evidence in respect to their possible derivation from one another or from common ancestral types. It appears that the processes which led to the definition of modern genetic groups also produced changes in karyotype so complex that an attempt to analyze them is not justified. Yet most of the distinctions in karyotype which differentiate the species within a genetic group are, with the exception of *glauca* and *longiflora*, relatively simple, and should be capable of cytogenetic analysis. The two exceptions demand further investigation concerning the methods and significance of their genom differentiation; and indeed the relation of *longiflora* to the 9-paired species of the ALATA-GROUP is now being studied.

BIVALENT CONFIGURATIONS IN NICOTIANA SPECIES

Although the bivalents in *Nicotiana* species are usually greatly contracted at IM, they nevertheless give evidence of the relationship between relative size and place of spindle-fiber insertion of the members of the karyotype and number and position of chiasmata. This relationship was first demonstrated in the ALATA-GROUP, where there are certain unusually distinct differences within the karyotypes in respect to chromosome length and insertion region. A series of trisomic plants in which the extra chromosome could be identified in somatic plates made it possible to follow through the late prophases and the metaphases of meiosis trivalent configurations of chromosomes the morphology of which was known. These configurations were then used in interpreting the bivalent configurations in diploid plants. These studies have established the following general relations between somatic morphology, the formation and terminalization of chiasmata, and the bivalent configurations at diakinesis and metaphase: (1) Large chromosomes with median insertion region (M) form at least one chiasma in each arm; by IM these chiasmata are usually completely terminalized so as to give a ring bivalent. Rarely, where more than one chiasma is formed in an arm an interstitial chiasma may persist until IM or, at times, a single chiasma may not be completely terminalized by IM. (2) Small chromosomes with median insertion region (m) may form a chiasma in each arm, or in one arm only; by IM these chiasmata are terminalized to give a small ring bivalent with two terminal chiasmata or an open ring or rod bivalent with one terminal chiasma. (3) Large chromosomes with submedian insertion region (SM) may form a chiasma in each arm which terminalizes by IM so as to give a ring bivalent with two terminal chiasmata, or the chiasma in the longer arm may fail to be completely terminalized; frequently a chiasma forms in the longer arm only and often is not completely terminalized by IM. (4) Small chromosomes with submedian insertion region (sm) behave as do "m" chromosomes, but may more frequently form a chiasma in one arm only, which is completely terminalized by IM so as to give a rod bivalent with one chiasma. (5) Chromosomes with subterminal insertion region usually form one chiasma only, which is terminalized to different degrees by IM to give "X," "+," or rod bivalents with one chiasma. The chiasma in a bivalent of small chromosomes (st) is more frequently completely terminalized than in a bivalent of large chromosomes (ST), and the latter may at times form two chiasmata.

TABLE 4

FREQUENCY AND POSITION OF TERMINAL (TERM.) AND INTERSTITIAL (INTER.) CHIASMATA (xta) AT IM IN FOUR SPECIES OF NICOTIANA

(Cf. Fig. 2)

	Insertion region	No. of chms.	No. of xta per chm.	No. of term. xta	No. of inter. xta	Total no. II_s x xta	Total xta
longiflora	ST	2	2	1	1	4	
(n=10)	ST+st	8	1	(1)	1	8	12
alata	M	2	2	2 (1)	(1)	4	
(n=9)	m	3	2 (1)	2 (1)	....	5 (6)	
	$ST+ST_s$	4	1	(1)	1	4	13
glauca	M	1	2	2	....	2	
(n=12)	m	1	1 (2)	1 (2)	....	1 (2)	
	$ST+ST_s$	10	1	(1)	1	10	13
glutinosa	M	4	2	2	....	8	
(n=12)	$SM+SM_s$	3	2	2 (1)	(1)	6	
	m+sm	5	2 (1)	2 (1)	....	8 (10)	22

Bivalent configurations in a few other species have been studied, and where it has been possible to correlate them with the corresponding karyotypes, the general relations enumerated above have been found to hold. This point is illustrated in table 4 and figure 2. Thus, in 10-paired *longiflora* (table 4) the total number of chiasmata at IM is less than the number in 9-paired *alata* because the former has all ST or st chromosomes in which, usually, only a single chiasma is formed, while half the genom of the latter consists of M or m chromosomes in most of which two chiasmata are formed. Similarly the total number of chiasmata in 12-paired *glauca,* with predominantly ST chromosomes, equals that in *alata* and is strikingly less than that in 12-paired *glutinosa* which has only M, m, SM, and sm chromosomes. The bivalents at diakinesis in *glutinosa* are usually rings with two chiasmata, while in *glauca* and

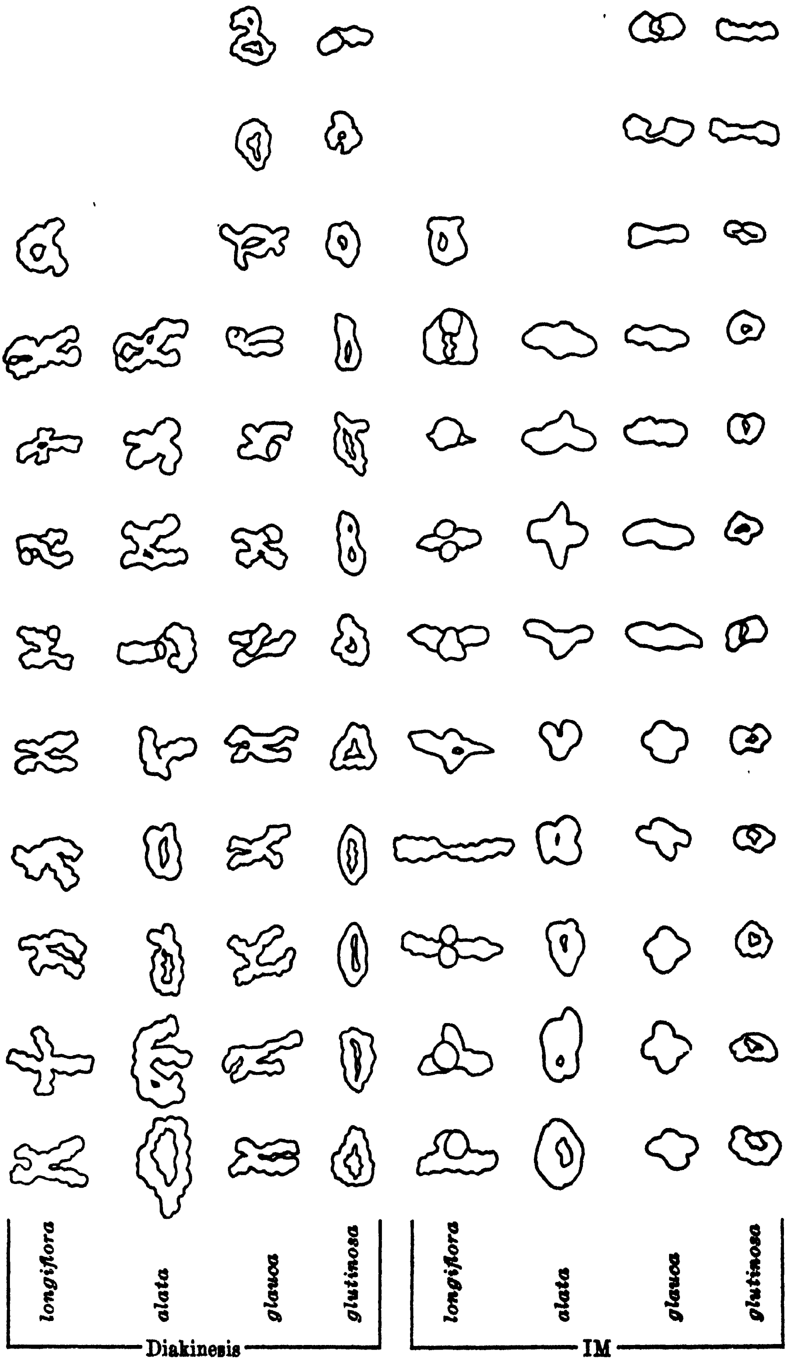

Fig. 2. Bivalent configuration, chiasma frequency and position, as determined by chromosome length and insertion region at diakinesis and IM in four species of *Nicotiana* (cf. table 6). The bivalents of a single PMC of each species are arranged in a horizontal row. The second *glauca* bivalent in diakinesis is a heteromorphic pair.

longiflora they are nearly all X, +, and rods with a single chiasma. In *alata* both types of configuration occur. Configurations at IM in these four species may also be contrasted. Thus, for example, all the bivalents except two in *glutinosa* have two terminal or nearly terminal chiasmata whereas in *glauca* only one pair has two terminal chiasmata. While the mode and significance of chiasma formation and terminalization in the various species of *Nicotiana* needs more comprehensive investigation, especially in respect to the relation between the earlier and later prophase stages, it is clear that there are differences in bivalent configuration and that these differences are definitely related to distinctions in chromosome length and insertion region. Thus, although certain species of *Nicotiana*, in common with those of other Solanaceous genera, have terminalized chiasmata producing droplet-like bivalents at IM, this is, as already indicated, by no means true of all bivalents of all species.

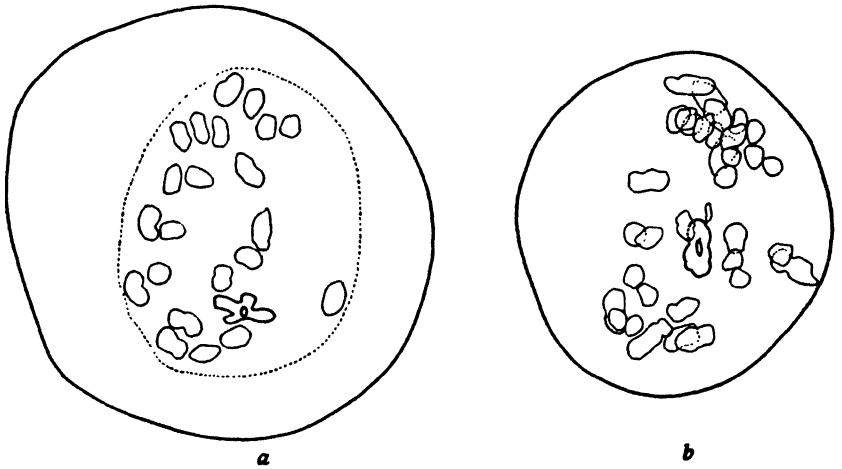

Fig. 3. *a*, F_1 *N. paniculata* × *N. Cavanillesii*, late diakinesis, $1_{II} + 22_{I}$, the bivalent with an interstitial chiasma. At IM in this hybrid there are usually no bivalents, or one bivalent with a terminal chiasma. *b*, F_1 *N. nudicaulis* × *N. glauca*, IM, $1_{II+f} + 34_{I}$, the bivalent composed of large *glauca* chromosomes with fragment (f) attached, being a product of translocation within the *glauca* genom; 12 larger *glauca* and 24 smaller *nudicaulis* chromosomes can be distinguished.

CHROMOSOME BEHAVIOR IN INTERSPECIFIC HYBRIDS

Previous reports relating to chromosome behavior in interspecific hybrids of *Nicotiana* have been sufficiently divergent so that it appeared essential in all possible hybrids to obtain evidence, at least of the amount of pairing at IM–IA, of statistical significance. In table 5 the character of the pairing at IM in twelve F_1 hybrids between 12-paired, eight between 24-paired and 12-paired, one between 24-paired and 16-paired,

TABLE 5

NUMBER OF BIVALENTS AT IM IN INTERSPECIFIC HYBRIDS OF NICOTIANA

	Fig.	0	1	2	3	4	5	6	7	8	9	10	11	12	Total
A. PAIRING IN HYBRIDS BETWEEN 12_{II} SPECIES															
paniculata × Cavanillesii	3*a*	*34*	12	4											50
Raimondii × glauca		*34*	8	5	3										50
glauca × Cavanillesii		*6*	1	2	3										12
glutinosa × sylvestris		6	*17*	*22*	3	2									50
paniculata × glutinosa		2	7	*14*	*17*	9	1								50
tomentosa × sylvestris	9*a–c*	4	11	*11*	*12*	5	4	2	1						50
trigonophylla × tomentosiformis		6	3	4	*10*	7	3	....	....	1	1				35
paniculata × undulata	5	1	3	10	*5*	*15*	9	3	4						50
glutinosa × wigandioides	8*a*	....	1	3	4	*13*	*9*	*11*	6	2	1				50
glutinosa × tomentosa (*a*)		....	....	2	9	*9*	*10*	*10*	6	3	1				50
(*b*)*		....	....	2	12	*22*	*25*	*18*	10	9	2				100
trigonophylla × tomentosa		....	....	1	1	....	....	....	7	*7*	*8*	8	3		35
paniculata × solanifolia	4	....	....	....	....	....	....	....	....	....	....	2	19	*29*	50
B. PAIRING IN HYBRIDS BETWEEN 24_{II} AND 12_{II} SPECIES															
Bigelovii var. multivalvis × sylvestris		*22*	20	8											50
Bigelovii var. Wallacei × glauca	12*a*	*71*	28	11	3										113
paniculata × Tabacum		*14*	11	10	9	6									50
rustica × Miersii		*13*	6	9	5	2									35
nudicaulis × glauca	3*b*	1	*11*	4											16
Bigelovii var. multivalvis × solanifolia	6	7	*16*	*15*	9	3									50
Tabacum × glutinosa	7*a*	3	8	*12*	*11*	*7*	3	4	1	1					50
rustica × wigandioides		....	5	*6*	*7*	*6*	3	....	2	1					30

* Elvers (1934). These 100 counts of the same hybrid are included to show the close correspondence in distribution to the 50 counts reported here.

TABLE 5—(*Concluded*)

	Fig.	0	1	2	3	4	5	6	7	8	9	10	11	12	Total
C. Pairing in a Hybrid Between 24_{II} and 16_{II} Species															
Bigelovii var. multivalvis × suaveolens		*24*	20	5	1										50
D. Pairing in Hybrids Between 24_{II} Species															
Debneyi × nudicaulis		7	12	*14*	10	5	2								50
rustica × Tabacum	7*b*	17	18	*22*	*24*	12	11	3	3						110
Bigelovii var. multivalvis × Tabacum		1	3	3	*6*	*7*	3	2							25

and three between 24-paired species is recorded. A total of twenty-four F_1 hybrids is included and investigation of as many more is nearing completion. With respect to a few, only a small number of chromosome counts are at present available, and these preliminary diagnoses are included because of the special significance of the hybrids involved.

In table 5A the amount of pairing in hybrids between twelve out of a total of nineteen known 12-paired species has been so arranged that the amount of pairing increases from *paniculata* × *Cavanillesii* (fig. 3*a*[*]), in which there is practically none, to *paniculata* × *solanifolia* (fig. 4), in which it is virtually complete. It is clear that certain of those species which have been combined on other grounds into genetic groups exhibit a higher degree of pairing when crossed than do hybrids between species assigned to different genetic groups. Thus, if the hybrids on the two sides of the dotted line running between 3 and 4 pairs are contrasted, it will be seen that, with one exception, the modes on the left are of hybrids the parents of which belong to different groups or to no recognized group, while the modes on the right side of the line are, also with one exception, characteristic of hybrids the parents of which belong to the same genetic group, with *paniculata* × *undulata* on the dividing line. The significance of pairing, especially as shown at IM, in suggesting species relationships has been questioned, and in particular it is said that little weight can be assigned to lack of pairing in interspecific hybrids since inherited asynapsis[†] (or "desynapsis") can occur. On the contrary, the reverse of the asynaptic picture has not been stressed as it should be—that is to say, apart from what is known as nonhomologous association (McClintock, 1933), there is no evidence to show that the occurrence of a significant amount of pairing is not a reflection of a corresponding amount of genic equivalence or similarity. Again, there is no justification for a disbelief in the significance of pairing as indicative of relationships in *Nicotiana* because in other material the evidence at present may not warrant such a conclusion.

For the hybrids listed in table 5 it is to be noted that, virtually always, no one number of pairs is the mode of the distribution. Thus, two or three numbers of pairs may constitute the classes with the greatest number of bivalents, with the classes above and below approximately equal in number of PMC. The major classes are italicized in the table. In a few hybrids between 12-paired species the very rare occurrence of a trivalent has been observed but such trivalents have not been separately classified in table 5A and are recorded as bivalents. In hybrids showing a minimum amount of pairing, chromosome fragments have rarely been observed at IM. Such fragments have not been recorded in table 5 but will be discussed in a more comprehensive report of chromosome behavior in these and in other hybrids.

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[*] In this and the following figures of IM in interspecific hybrids, bivalents are outlined more heavily than univalents.

[†] The nature of an X-ray-induced gene alteration leading to asynapsis in *N. sylvestris* has been the subject of extended investigations in this laboratory (unpublished), so that the background for this criticism is fully appreciated.

It will be seen in table 5A that the hybrids showing a minimum and a maximum amount of chromosome conjugation have ranges extending over three to four classes, while those showing an intermediate amount have ranges extending over six to ten classes. In these hybrids it is also to be noted that as the mode becomes higher the lowest classes are not represented, even though the total range is great. In hybrids between 24-paired and 12-paired species pairing falls into two distinct groups, by contrast with the situation in hybrids between 12-paired species just commented upon. Thus, in eight hybrids (table 5B) the modal classes do not exceed four pairs, while, with one exception, for the eight hybrids in table 7, the mode is twelve pairs or its equivalent. This distinction in mode in tables 5B and 7 may be less sharp when other hybrids are investigated. Indeed, the range of pairing in *trigonophylla* × *nudicaulis* and *rustica* × *solanifolia* is a step in this direction.

TABLE 6

NUMBER AND POSITION OF CHIASMATA (xta) AT IM IN BIVALENTS FORMED IN 50 PMC OF EACH OF FOUR INTERSPECIFIC HYBRIDS OF N. PANICULATA

	No. of II_s in 50 PMC	No. of Term. xta	No. of Int. xta	No. of Undet. xta	Total xta
paniculata × Cavanillesii	20	15	4	1	20
paniculata × glutinosa	127	65	62	3	130
paniculata × undulata	189	97	91	17	205
paniculata × solanifolia	577	720*	288*		1008*

* Estimated from analysis of a few IM plates which show that where 12II occur, about 15 terminal and 6 interstitial chiasmata are formed.

While table 5A shows the range and variation in the amount of pairing in hybrids between 12-paired species, it does not show the differences in the character of the pairing which occur, and in terms of phylesis these may be of significance. Thus the range in kinds of bivalents formed extends from the few "loose" pairs with a single terminalized chiasma in *paniculata* × *Cavanillesii* to the 12 "close" pairs in *paniculata* × *solanifolia* (fig. 4), nine of which usually have two chiasmata. The correlation between increase in number of pairs and increase in number of chiasmata is shown in table 6, where the bivalents recorded in fifty PMC of each of four different interspecific hybrids of *paniculata* are classified in respect to number and position of chiasmata. Here the same species was always the female parent, and the other species used are all 12-

paired. The fact that in these hybrids, as in all other hybrids here reported on, the analyses at IM were made from PMC of various anthers, various buds, often of several different plants, some collected at different times, and the observations recorded by two different persons gives assurance that the results are typical.*

We may conclude from table 6, that in interspecific hybrids of *Nicotiana* the following relations between bivalent formation and chiasma behavior hold: (1) The bivalents in hybrids showing the minimum

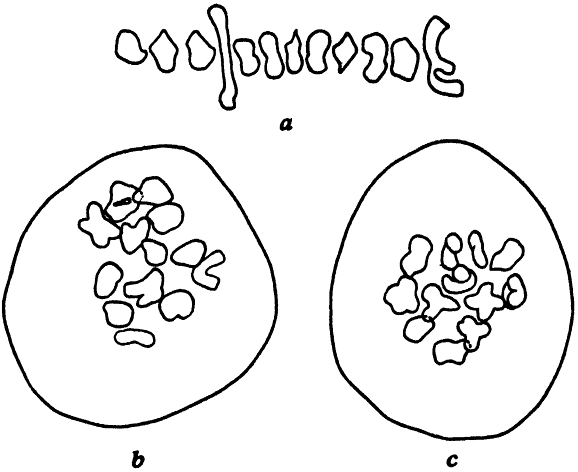

Fig. 4. F_1 *N. paniculata* × *N. solanifolia*. *a*, IM, side view, 12_{II} drawn separately showing one characteristic bivalent with interstitial chiasma, and another with one terminalized chiasma. *b*, IM, polar view, $11_{II} + 2_{I}$, the two univalents of different size. *c*, IM, polar view, 12_{II}, of which 9_{II} have 2 and 3_{II} have 1 chiasma.

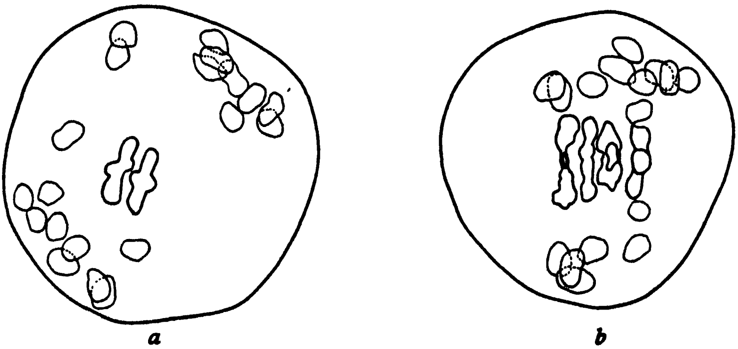

Fig. 5. F_1 *N. paniculata* × *N. undulata*, IM. *a*, $2_{II} + 20_{I}$. *b*, $4_{II} + 16_{I}$, 1_{II} with two terminal chiasmata, and 1_{II} with one interstitial chiasma.

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* The fact that only bivalents are recorded in tables 5, 6, and 7 does not mean that they alone were counted. With the exception of hybrids between 24-paired species, and of 76 of the 113 counts of *Bigelovii* × *glauca* where the total number of univalents could not always be determined, the counts reported represent analyses of PMC in which every unit was interpreted.

amount of pairing usually form a single terminal chiasma, the total number of chiasmata equaling the number of bivalents (cf. figs. *3a*, *6b*, *7b*, *9a-c*). (2) With increase in number of bivalents there is a disproportionately greater increase in total number of chiasmata, because in certain of the bivalents two chiasmata are formed, and there is also an increase in the proportion of interstitial chiasmata (cf. *paniculata* × *undulata*, fig. 5). (3) With almost complete pairing, the total number of chiasmata approaches that in the parental species, a slight reduction in such a hybrid as *paniculata* × *solanifolia* probably resulting from

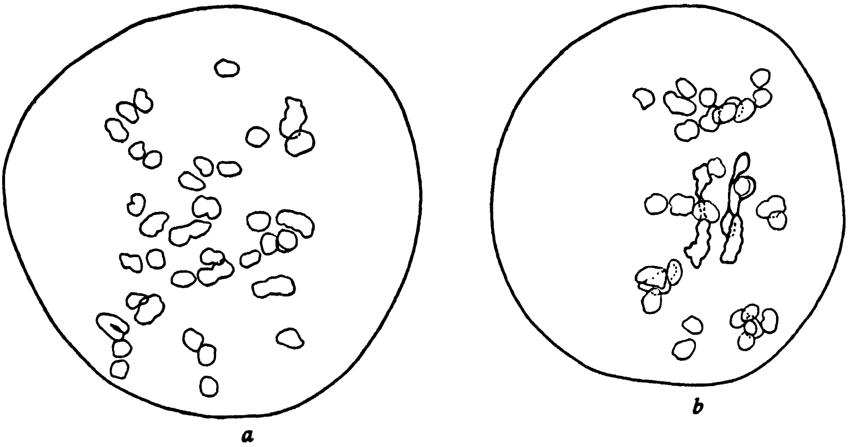

Fig. 6. F_1 *N. Bigelovii* var. *multivalvis* × *N. solanifolia*, IM. *a*, 24_{I}, of which 12 are larger *solanifolia*, and 24 smaller *Bigelovii* chromosomes. *b*, $3_{II} + 30_{I}$, all bivalents with a single terminal chiasma, 2_{II} consisting of one larger *solanifolia* and one smaller *Bigelovii* chromosome, and 1_{II} of two smaller *Bigelovii* chromosomes.

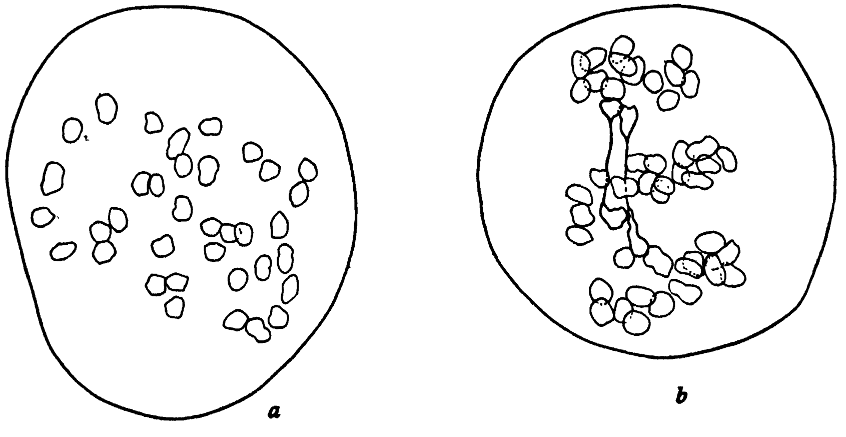

Fig. 7. *a*, F_1 *N. Tabacum* × *N. glutinosa*, IM, 36_{I}. *b*, F_1 *N. rustica* × *N. Tabacum*, IM with $2_{II} + 44_{I}$, showing univalents distributed in three groups, and bivalents each with one terminalized chiasma.

chromosomal rearrangement, as evidenced by the inequality in size of the two univalents in PMC where only eleven pairs are formed (fig. 4*b*), and the occasional formation of a trivalent or, more rarely, of a quadrivalent.

The evidence contained in tables 5, 6, and 7 leads to the following interpretations of the relation of chromosome behavior in interspecific hybrids to phylesis: (1) When two chromosome complements are capable of coöperating so that a normal soma is built, these chromosome sets have at least residual homology and presumably contain genes in common. (2) Association between all the chromosomes present to produce bivalents is positive evidence that these chromosomes possess many similar or equivalent genic elements and that the species involved are closely related. (3) A decrease in the amount of pairing characteristic of postulate (2) is to be related to an accumulation of genic and chromosomal distinctions between species evolved from a common stock. (4) The minimum amount of pairing bears a definite relation to the number of chromosomes present and may be a reflection of (*a*) residual homology possessed by races the progenitors of which were more closely related than those races are today; (*b*) the occurrence of nonhomologous association at pachytene. (5) The line of demarcation between postulates (3) and (4) cannot be sharply drawn, but steps in reduction in the amount of pairing are significant as indicating progressive decrease in relationship however originating or accomplished, the ultimate reduction to consistent and complete lack of pairing being unattainable because of residual homology and nonhomologous association. It is contended that, bearing in mind the difficulties in rigorously applying such specific postulates, the correspondence in the genus *Nicotiana* between the evidence of relationship among its species provided by external morphology and by the extent and character of the pairing at IM is too marked to be disregarded.

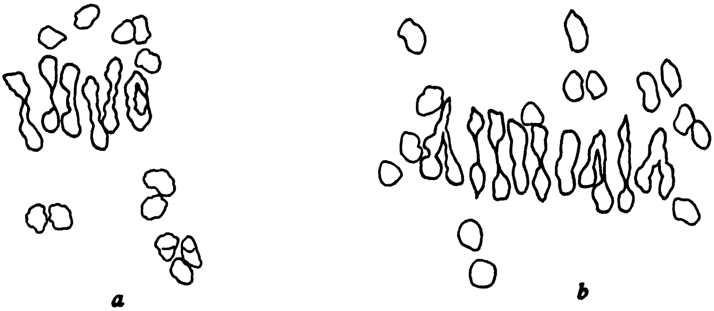

Fig. 8. Bivalents and univalents drawn separately. *a*, F_1 *N. glutinosa* × *N. wigandioides*, $6_{II} + 12_{I}$. *b*, F_1 *N. trigonophylla* × *N. nudicaulis*, $3_{III} + 6_{II} + 15_{I}$.

SIGNIFICANCE OF AMPHIDIPLOIDY IN NICOTIANA

The third type of evidence noted in the Introduction as bearing upon phylesis in *Nicotiana* involves initial hybridization between species followed by the attainment of a balanced chromosomal condition. Such a balanced condition follows the building of a hybrid soma from cell lines originating in a suspended early zygote or other mitosis or the production of a zygote following union of somatic gametes. The resulting individual is in either event an amphidiploid and such types are of remarkably frequent occurrence in *Nicotiana*. Thus the amphidiploids "digluta" (*glutinosa* × *Tabacum*), "diglutosa" (*glutinosa* × *tomentosa*), "disualovii" (*Bigelovii* × *suaveolens*) have occurred in our cultures and a number of others have been reported elsewhere (cf. Kostoff, 1933; Winge, 1932; Ternovsky [in correspondence]). From their first appearance these "synthetic" species are chromosomally balanced as a result of pairing between the two sets from each parent which are present. A somatic gamete of either parent of an interspecific hybrid or the cross of one of the original parental species with an amphidiploid produces a sesquidiploid and it is potentially of significance with reference to the origin of new chromosome numbers and new morphological types.

Whatever may be the significance of amphidiploidy in interpreting species origins and relationships in other genera, it is very real in *Nicotiana*. Undoubtedly the growing of a sufficient number of individuals of any F_1 interspecific *Nicotiana* hybrid would yield amphidiploids, and the frequency of their occurrence under experimental conditions suggests the probability of their production in nature also. The situation brought out in table 7, together with the view just expressed, represents the basis for assuming that the 24-paired American species of *Nicotiana* are of amphidiploid origin.

In table 7, Drosera scheme behavior in hybrids between 24- and 12-paired American species is shown. Reference to table 5 will indicate chromosome behavior in other hybrids of these same species. The occurrence of trivalents and quadrivalents as well as pairs is shown and its significance will be commented upon in what follows.

Of the eight hybrids in table 7, the first five have been adequately studied and show Drosera scheme behavior, while the remaining three, with less extensive counts, represent such behavior or a modification of it. Drosera scheme behavior has already been reported in *Tabacum* × *sylvestris* and *rustica* × *paniculata* and these reports are confirmed. The occasional occurrence in these two hybrids of one trivalent and rarely two may be ascribed to residual homology or nonhomologous associa-

TABLE 7

NUMBER OF PAIRS IN HYBRIDS BETWEEN 24_{II} AND RELATED 12_{II} SPECIES

	Fig. No.	6	7	8	9	10			11				12												Total
						10	$9_{II}+1_{III}$	$8_{II}+2_{III}$	11	$10_{II}+1_{III}$	$9_{II}+2_{III}$	$8_{II}+3_{III}$	12	$11_{II}+1_{III}$	$10_{II}+2_{III}$	$8_{II}+4_{III}$	$9_{II}+1_{III}+1_{IV}$	$10_{II}+1_{IV}$	$9_{II}+1_{VI}$	$8_{II}+1_{VI}+1_{III}$	$7_{II}+1_{VI}+1_{IV}$	$8_{II}+2_{IV}$	$7_{II}+2_{IV}+1_{III}$	$9_{II}+2_{IV}$	
Tabacum × sylvestris	9*d*, *e*				1	2			1	3			*32*	12	1										52
Tabacum × tomentosa	9*f*													*26*	2		17	5							50
Tabacum × tomentosiformis	11*a*, *d*													*31*	19										50
rustica × paniculata													*39*	10	1										50
rustica × undulata	11*b*, *c*												3				6	*15*	*14*	3	4	2	2	1	50
rustica × solanifolia	10				3	5	1	1	5	1	1	1	*11*	4	4										37
Bigelovii var. multivalvis × attenuata	12*b*								1	1			*3*	1	1	1									8
trigonophylla × nudicaulis	8*b*	1	1	2	*3*	1			1				1												10

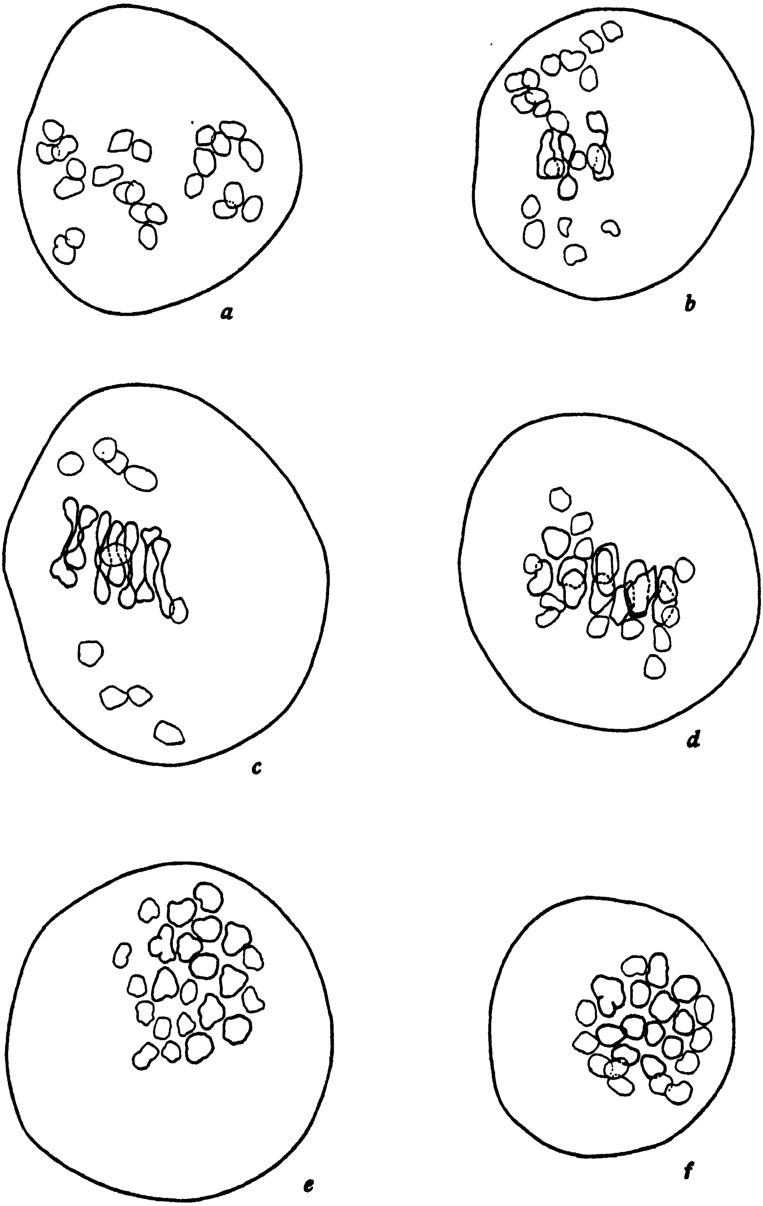

Fig. 9. IM in F_1 hybrids of the Tabacum-triangle. *a-c*, F_1 *N. tomentosa* × *N. sylvestris* with *a*, 24_{I}, *b*, $3_{II} + 17_{I} + 2_{f}$, and *c*, $7_{II} + 10_{I}$. *d* and *e*, F_1 *N. Tabacum* × *N. sylvestris*, with *d*, $12_{II} + 12_{I}$ in side view, and *e*, $1_{III} + 11_{II} + 11_{I}$ in polar view. *f*, F_1 *N. Tabacum* × *N. tomentosa*, $1_{III} + 11_{II} + 11_{I}$ in polar view.

tion. It is doubtful whether the finding of a few PMC with less than 12_{II} in *Tabacum* × *sylvestris* has any special significance, but it could be accounted for if the nonhomologous association of unpaired chromosomes occasionally prevents the formation of homologous pairs (McClintock, 1933).

The presence of at least one trivalent in *Tabacum* × *tomentosa* (fig. 9*f*) and *Tabacum* × *tomentosiformis* (fig. 11*a*, *d*) which involves conjugation of a member of the *sylvestris* subgenom of *Tabacum* with a bivalent made up of a member of the *tomentosa* or *tomentosiformis* subgenom with *tomentosa* or *tomentosiformis*, may be interpreted as evidence of reciprocal translocation within the *Tabacum* complement. By contrast with trivalent formation in these hybrids is the occurrence of quadrivalents or sexavalents in *rustica* × *undulata* (fig. 11*b*, *c*). As will be noted in table 7, in only three out of fifty PMC were no valencies higher than two formed. Typically a ring quadrivalent is seen, but often a bivalent is associated with the ring (fig. 11*b*, *c*). Such association can best be interpreted on the basis that translocations within the *undulata* set have occurred. In this connection attention is directed to fig. 3*b*, showing a bivalent which was uniformly formed between two members of the *glauca* genom in the hybrid with *nudicaulis*. This fact confirms other evidence which points to the occurrence of translocation within the *glauca* complement. These evidences of chromosome interchange appearing in interspecific hybrids and not suspected in the parental species, point to interspecific hybridization as a means of bringing to light such significant changes within a genom.

All the crosses referred to in tables 5B and 7 except *paniculata* × *Tabacum* and *trigonophylla* × *nudicaulis* have been obtained with the 24_{II} species as female parent and in only a very few have reciprocal hybrids been produced. This result is in accord with experience in this genus and elsewhere (cf. Thompson, 1930).

That *N. Tabacum* is of amphidiploid origin, with the progenitors of modern *tomentosa* and modern *sylvestris* as the parental species, was suggested some years ago (Goodspeed and Clausen, 1928), the finding of the amphidiploid "digluta" (Clausen and Goodspeed, 1925) having provided first proof of the basic hypothesis offered by Winge (1917). Additional confirmatory evidence in respect to the postulated origin of *Tabacum* has since been produced (Clausen, 1928, 1932; Brieger, 1930; Kostoff, 1931). Of some special interest was the discovery of "diglutosa," an amphidiploid between two 12-paired *Nicotiana* species (Goodspeed, 1933; Elvers, 1934). On the basis of these data and the additional evidence here submitted, there is thorough justification for the following conclusions: (1) Some progenitor of the TOMENTOSA-GROUP, now known to be represented by *tomentosa*, *tomentosiformis*, *glutinosa*, and *wigandioides,* entered into the production through amphidiploidy of the highly polymorphic modern species called *Tabacum.* Of the members of the TOMENTOSA-GROUP, *tomentosa* and *tomentosiformis* appear to be genetically closest to the ancestral races, on the basis particularly of chromosome behavior in interspecific hybrids within the group (cf. fig. 8*a*) and between its members and *Tabacum.* (2) A progenitor of modern *sylvestris* represents the other parental race in the amphidiploid origin of *Tabacum.* That *sylvestris, tomentosa,* and *tomentosiformis* are the only species known to give Drosera scheme relations with *Tabacum* (cf., for example, lack of Drosera scheme behavior in *paniculata* × *Tabacum,* *Tabacum* × *glutinosa,*[*] table 5B), and that these species show such behavior only with *Tabacum* (cf., for example, *Bigelovii* × *sylvestris,* table 5B) is the strongest confirmation of this and the first conclusion. (3) An amphidiploid hybrid between *tomentosa* or *tomentosiformis* and *sylvestris* would not necessarily represent the genetic complex of modern *Tabacum,* as has been shown by Brieger (1930) and Kostoff (1933). In other words, the original postulate (Goodspeed and Clausen, *loc. cit.*) made no assumption that the modern representatives of the "Tabacum-triangle" were identical genetically with the original parents or with the initial forms of the amphidiploid product, a point apparently overlooked by Kostoff (1933). Bearing directly upon this matter is the evidence, already commented upon, that a trivalent uniformly occurs at IM in *Tabacum* × *tomentosa* (fig. 9*f*) and *Tabacum* × *tomentosiformis* (fig. 11*d*).

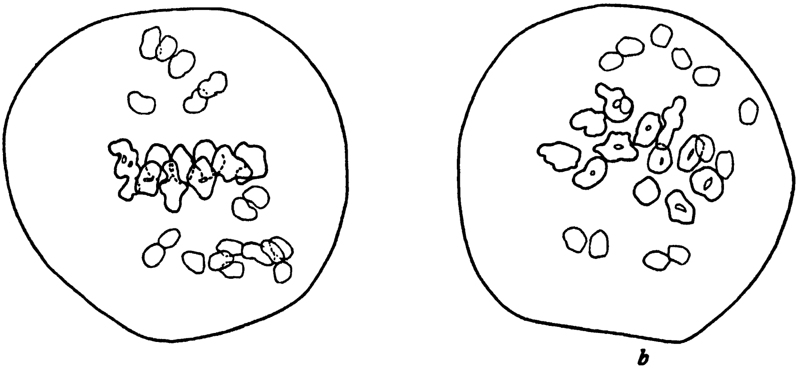

Fig. 10. F_1 *N. rustica* × *N. solanifolia,* IM. *a,* $9_{II} + 18_{I}$ in side view. *b,* $12_{II} + 12_{I}$ in polar view. A characteristic bivalent with one interstitial chiasma similar to a bivalent characteristic of F_1 *paniculata* × *solanifolia* (fig. 4) is evident in both *a* and *b.*

It is now possible to parallel the evidence available respecting the origin of *Tabacum* with evidence respecting the origin of *rustica,* another highly polymorphic 24-paired *Nicotiana* species. As indicated earlier, the PANICULATA-GROUP is well defined, except *glauca*. Thus, the basic relationships between *paniculata, solanifolia, Raimondii,* and *undulata* are undoubted. Chromosome behavior at IM (tables 5A and 7) in hybrids within the PANICULATA-GROUP and between members of this group and *rustica* makes it clear that progenitors of modern *paniculata* and modern *undulata* entered into the amphidiploid origin of *rustica*. The species *solanifolia,* like *tomentosiformis* in the Tabacum-triangle, presumably could be substituted for *paniculata* (fig. 10), although genetically these two members of the PANICULATA-GROUP do not appear to be as closely related as are *tomentosa* and *tomentosiformis*. As in the Tabacum-triangle, Drosera scheme relations obtain in the F_1 hybrids of *paniculata* and *undulata* with *rustica,* as compared with chromosome behavior in *paniculata* × *Tabacum, rustica* × *Miersii,* and *Bigelovii* × *solanifolia* (tables 5A and 7; fig. 6). In addition, it has been possible to secure trigenomatic *paniculata-undulata-rustica* plants which show 24_{II} and are fertile. Finally, in the "rustica-triangle" the presence of a quadrivalent or sexavalent in F_1 *rustica* × *undulata* (fig. 11*b, c*) makes it clear that, just as in the Tabacum-triangle, chromosome reorganization has occurred either in the parental species or in their amphidiploid

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[*] East (1933) reports Drosera scheme behavior in *Tabacum* × *glutinosa,* results which we have been unable to confirm (cf. fig. 7*a*).

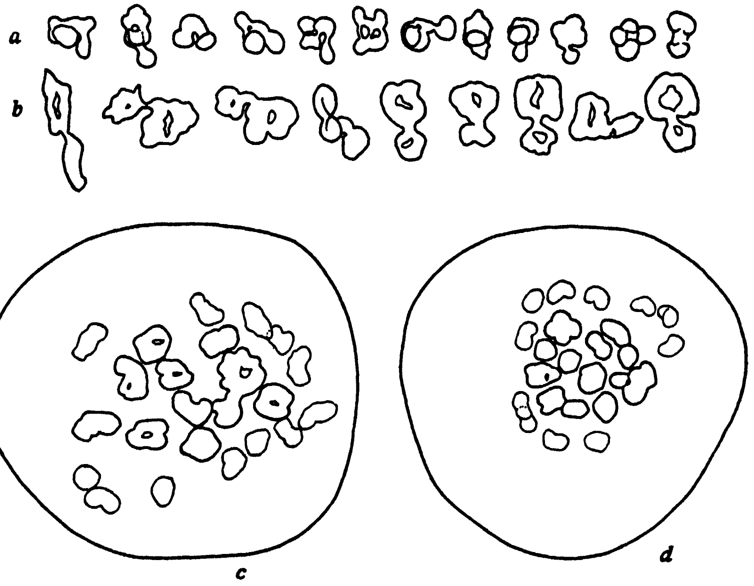

Fig. 11. *a,* Trivalents from 12 different PMC of F_1 *N. Tabacum* × *N. tomentosiformis. b,* Sexavalent from 9 different PMC of F_1 *rustica* × *undulata,* showing typical formation of a ring quadrivalent and its association with another bivalent. *c,* F_1 *N. rustica* × *N. undulata,* IM, $1_{VI} + 9_{II} + 12_{I}$. *d,* F_1 *N. Tabacum* × *N. tomentosiformis,* IM, $1_{III} + 11_{II} + 11_{I}$.

product, since the origin of the latter. The combined evidence thus justifies the conclusion that modern *rustica* is of amphidiploid origin, the original parental species being progenitors of members of the modern PANICULATA-GROUP, and probably of *paniculata* and *undulata,* and that the modern species making up the rustica-triangle are not genetically equivalent to the ancestral races.

Little evidence is available (table 7) respecting the origin of *Bigelovii* and *nudicaulis,* but it suggests that a progenitor of *attenuata* entered into the production of the highly polymorphic species *Bigelovii* by amphidiploidy (cf. fig. 12). In respect to *nudicaulis,* concerning the polymorphism of which little is known, it is suggested that its origin was also by way of amphidiploidy involving a member or members of a genetic group of species to which *trigonophylla* belongs (cf. fig. 8*b*). Apparently *trigonophylla* is related to the ancestral species actually involved in the origin of *nudicaulis* more closely than is *glutinosa* to the TOMENTOSA-GROUP progenitors of *Tabacum* and somewhat less closely than is *solanifolia* to the *paniculata*-like ancestor of *rustica.*

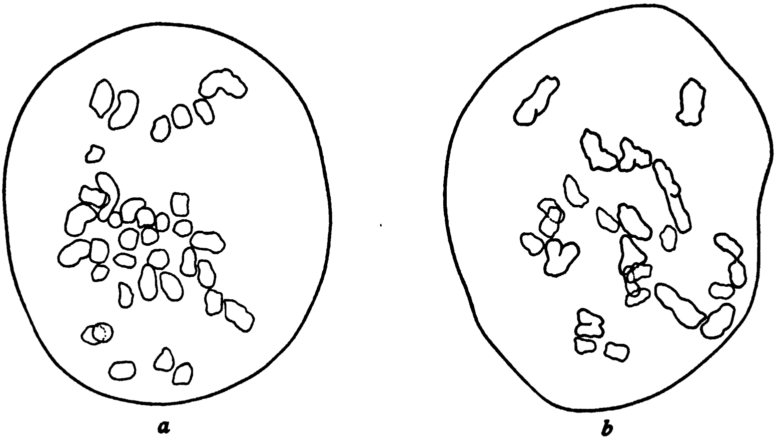

Fig. 12. *a,* F_1 *N. Bigelovii* var. *Wallacei* × *N. glauca,* early IIM in a PMC in which no interphase followed IA distribution of unpaired chromosomes; 12 larger *glauca* and 24 smaller *Bigelovii* chromosomes are to be seen. *b,* F_1 *N. Bigelovii* var. *multivalvis* × *N. attenuata,* early IM, $12_{II} + 12_{I}$.

It is evident that *Nicotiana* is favorable material in which to study evidences of phylesis in a representative genus of higher plants. The current taxonomic arrangement of the genus is inadequate because it is based upon imperfect evidence in respect to important morphological criteria. A forthcoming taxonomic revision of *Nicotiana* in the light of new evidence will be an end in itself, but is looked upon as a means to the end that, when supplemented by pertinent cytogenetic and other data, a partly complete statement of basic genetic relationships and modes of species origin will be possible. Thus it is hoped that not only will the genus become more intelligible from the strictly morphological-taxonomic point of view, but that in addition a demonstration of the modes of phylesis operating in the past will be possible.

The author gratefully acknowledges the assistance and advice of Drs. P. Avery and D. R. Cameron and the constant encouragement of Professor W. A. Setchell, who thirty years ago originally undertook the *Nicotiana* investigations which have been carried on continuously since that time in the University of California Botanical Garden.

While this paper was in press, the following pertinent cytological and genetic studies on *Nicotiana* appeared: Eghis, S. A., Bull. Applied Bot. and Plant Breeding, Ser. II-d, No. 5:108–125, 1933; Woycicki, Z., Acta Soc. Bot. Poloniae, 10:441–449, 1933; Sarana, M. O., Inst. Tob. Ind. U.S.S.R., Bull. No. 110:185–190, 209–220, 224, Krasnodar, 1934.

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NEW OR LITTLE KNOWN WEST AMERICAN WILLOWS

BY

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NEW OR LITTLE KNOWN WEST AMERICAN WILLOWS

BY

CARLETON R. BALL*

REVISIONS of the Salices of California and of the Alaska-Yukon Territory region are in preparation. Abundant collections were available and much new material has been collected especially for this purpose in the past three seasons. Among the recent collections from the two named areas and from other western districts are several previously undescribed species and varieties. Some of them belong to sections of the genus, the revision of which cannot be completed for an indefinite time. As named specimens of some of these have already been distributed widely, their descriptions should be published without further delay. One species, *S. Farrae* Ball, previously described briefly, is presented in full detail.

It is a pleasure to acknowledge the many courtesies and whole-hearted assistance received in the course of these studies from the staff of the Department of Botany of the University of California, and especially from Professor W. A. Setchell, and to acknowledge as well courtesies from those in charge of other herbariums and from many professional and amateur botanists and nature lovers throughout the country. Never, it seems to me, has a specialist received more abundant and hearty cooperation. Specific and full acknowledgment of the varied services of individuals and institutions is set forth in the introduction to the monographic studies, two parts of which are nearing completion.

LIST OF HERBARIUMS HOUSING THE COLLECTIONS

The following initials have been used to designate the herbariums in which the collections examined are housed.

AA	Arnold Arboretum
CAS	California Academy of Sciences
CRB	Carleton R. Ball
GH	Gray Herbarium of Harvard University
NMC	National Museum of Canada
PANS	Philadelphia Academy of Natural Sciences
RMP	Rocky Mountains Park Herbarium at Banff
UAC	Utah Agricultural College
UC	University of California
USN	United States National Herbarium

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* Research Associate, Bureau of Public Administration, University of California.

Salix Parksiana n. sp.

Plates 67 and 68

Section *Longifoliae.* Frutex, 1.5–3 m. altus; ramulis obscure brunneis, plerumque pilosis; foliis anguste ellipticis, subsessilis, apice basique acutis, irregulariter et frequenter remote denticulatis, pilosis; amentis coetaneis, 4–8 cm. longis, solitariis aut 2–4 aggregatis, pedunculos longos foliosos aut surculos anni terminantibus; squamis florum ovatis obovatisve, stramineis, glabratis; staminibus 2, filamentis liberis, in dimidio basali dense undulato-pilosis; capsulis ovate-lanceolatis, 5 mm. longis, sessilibus subsessilibusve, glabris; stylo obsoleto, stigmatibus brevibus, divisis. Frondes multo ut in *S. sessilifolia* sed capsules multo ut in *S. melanopside.*

Low to midheight cespitose shrub, 3–10 ft. (1–3 m.) high, usually 4–6 feet; bark gray, branchlets brown to dark brown, seasonal and 1-year shoots densely, and 2-year shoots thinly to densely, pilose or pilose-tomentose with white hairs; lenticels small, 0.2–0.4 mm. wide, broadly oval to orbicular, hemispherical, projecting; bud scales 5–6 mm. long, obtusish, dark brown, thinly to densely pilose-tomentose.

Leaves exstipulate and sessile, except on vigorous shoots; stipules wanting on fruiting branchlets, lanceolate or semicordate to ovate, 2–4 or 5 mm. long, acute, denticulate, and pilose on vigorous shoots; petioles practically wanting on leaves of fruiting branchlets but 1–2 mm. long on shoots and occasionally 4–6 mm. long on very vigorous growth, pilose; blades usually narrowly to usually broadly elliptical, or occasionally elliptical-oblanceolate to oblong-elliptical, acute at both ends, abruptly tapering at base, often apiculate at apex or shoot leaves short-acute, 4–12 cm. long, 0.8–2.6 cm. wide, common sizes being in cm., 4 × 0.8–1.1, 5 × 1.2–1.5, 6 × 1.5–1.8, or 2.2, and 7–8 × 1.6–2 or 2.5 on fruiting branchlets, and 7 × 2.5, 8–9 × 2.7, 9–10 × 2.2–2.7, and 11–12 × 2–2.6 on vigorous shoots, irregularly and sometimes remotely glandular-denticulate on margins, the teeth sometimes spinulose and curved toward the leaf apex, both surfaces, including midrib and veins, densely to thinly pilose or pilose-tomentose with silvery hairs, sometimes concealing the teeth, the small inferior leaves sometimes glabrate.

Aments coetaneous, borne on elongated leafy seasonal shoots, solitary or in clusters of two to four, distal aments earlier than lateral in flowering; peduncles or seasonal flowering shoots 2–4 or 5 cm. long in flower, becoming 4–7 or 10 cm. long in fruit, and bearing 3–5 foliage leaves, of which one often subtends a secondary leafy shoot.

Staminate aments cylindrical, slender, 4–7 or 8 cm. long, 7–9 mm. wide, somewhat lax at base, yellow; flower scales elliptical-oblong to obovate, subacute to usually rounded or somewhat truncate, pale yellow, thinly pilose with crinkly hairs, becoming glabrate, especially on dorsal surface and toward apex; stamens 2, filaments free, 3–3.5 mm. long, densely pilose with crinkly white hairs on basal half or two-thirds.

Pistillate aments slender, often elongated, 4–6 or 8 cm. long in flower, becoming 4–9 (sometimes 11–13) cm. long in fruit, 1–1.4 cm. wide; flower scales oblong-ovate to ovate, acutish to obtuse, 2–3 mm. long, 3-veined, thinly pilose-tomentose when young, becoming glabrate on outside, especially toward apex; capsule narrowly ovate to ovate, from a subacute base, sessile to subsessile, 4.5–5 or 5.5 mm. long, brown, glabrous or ovary sometimes thinly pilose; pedicels 0.2–0.4 mm., or lowermost occasionaly 1 mm. long; style obsolete; stigmas short, 0.2–0.4 mm. long, divided, spreading; seeds linear-oblanceolate, about 0.8 mm. long, coma hairs 3–4 mm. long; gland 1, ventral, subcylindrical, slender, capitate, about 1 mm. long.

Salix Parksiana belongs to Section *Longifoliae,* the long-leaf or sandbar willows, so abundantly distributed over the western and part of the eastern United States, and from Mexico to Alaska and the Yukon Territory. The section is composed of two groups. One group, limited to the Pacific Coast, has pilose capsules, mostly evident styles, and long stigmas, and contains *S. fluviatilis* Nutt., *S. sessilifolia* Nutt., *S. Hindsiana* Bentham and its varieties, and *S. taxifolia* Kunth., the latter having almost no style. The second group, occupying nearly the entire continent, is distinguished by usually glabrous capsules (though the ovaries sometimes are pilose), obsolete styles, and usually short sessile stigmas. *S. Parksiana* belongs to this group, which contains *S. interior* Rowlee (*S. longifolia* Muhl.), *S. exigua* Nutt. and its many varieties, *S. melanopsis* Nutt. and its several varieties, and *S. argophylla* Nutt. The last three are confined to the western United States.

Salix Parksiana is most closely related to *S. melanopsis* Nuttall, and especially to its variety, *Bolanderiana* (Rowlee) Schneider, with leaves more or less pubescent-tomentose. In aments and capsules it differs scarcely at all from *melanopsis.* The large and markedly elliptical leaves, with their usually silvery pilose covering, however, are more similar to those of *S. sessilifolia* Nuttall. The limited known range of *S. Parksiana* is within the range of *S. melanopsis* and its varieties, and lies just at the southern end of the known range of *S. sessilifolia.* There is absolutely no evidence of hybridity, however, in the more than twenty sets of *S. Parksiana* collected in 1931.

It is a great pleasure to name this species in honor of my friends, Mr. Harold E. Parks and Mrs. Susan T. Parks, whose interest in the California flora has been of great help to many specialists. They are primarily responsible for the discovery of this willow and for the collection of that abundance of material which permits an adequate description and freedom from misgivings in respect to the validity of the species.

Types.—Staminate type collection is Parks No. 0983, gravel bars of Smith River near Roosevelt Highway Bridge, Del Norte County. Pistillate type is Parks No. 0962, in river gravels of Van Duzen River between Alton and Carlotta, Humboldt County. The type specimens are in the herbarium of the University of California (sheets Nos. 481288–481289 (♀), and 481366–481367 (♂)), and exactly similar cotypes are in the writer's herbarium. Specimens of both numbers were widely distributed to the leading herbariums of the world, under printed labels showing them to be the type collections.

Distribution.—*Salix Parksiana* is known only from a strip of coastal plain about one hundred miles long, in Humboldt and Del Norte counties, in extreme northwestern California. All the rivers of this area have their headwaters in the various minor ranges of the Coast Range, and in their lower reaches flow in a northwesterly direction into the Pacific Ocean. From south to north, the rivers reaching the ocean are the Eel, Mad, Klamath, and Smith, of which the Eel and Klamath are large streams with many tributaries. This willow has been collected on three of these systems. Van Duzen River is a small stream rising in the Coast Range and flowing west to join the Eel River near the ocean. Trinity River rises in the Coast Range and flows nearly due north into the Klamath, Willow Creek entering the Trinity from the west, not far above its mouth in northern Humboldt County. Smith River is a short stream rising in the Siskiyou Mountains, crossing the extreme northwestern corner of Del Norte County, and reaching the ocean near the Oregon boundary.

Habitat.—*Salix Parksiana,* like the closely related *S. melanopsis* Nuttall, is a plant of gravel bars, or rocky or sandy beds or banks of streams. Apparently it does not occur in alluvial meadows.

The specimens listed below have been examined. The arrangement is from south to north.

California. *Humboldt County.* Eel River at mouth of Larrabee Creek, alt. 200 ft., Joseph P. Tracy 10291 (♀), July 31, 1932 (CRB, UC). Van Duzen River, Bridgeville, alt. 750 ft., Tracy 10129 (♂), June 4, 1932 (UC). Van Duzen River between Alton and Carlotta, alt. 15 m., shrubs 1–2 m. high, in river gravel, Harold E. Parks 0961 (♂), 0962 (pistillate type), 0964 (♂), all May 14, 1931 (CRB, UC). Van Duzen River, Alton, alt. 100–300 ft., Tracy 9682, Sept. 19, 1931 (CRB, UC). Trinity River, shrub 2 m. high, on sand bars, mouth of Willow Creek at Trinity River, alt. 150 m., Parks and Tracy 0967, May 17, 1931 (CRB, UC).

Del Norte County. Smith River at or near Roosevelt Highway Bridge, about 5 miles above the mouth, alt. about 50 ft.: shrubs 1–2.5 m. high, on gravel bars, Harold E. Parks 0977 (♀), 0978 (♀), 0979 (♂), 0980 (♀), 0982 (♂), 0983 (staminate type), 0987 (♀), 0990 (♀), and 0992 (♀) (CRB, UC); shrubs 1–2.5 m. high, frequent in gravelly river margin, Parks and Tracy 01003 (♀), 01004 (♂), 01006 (♂), 01007 (♀), 01010 (♂), 01013 (♀), 01014 (♀), and 01015 (♀), all May 30, 1931 (CRB, UC); on gravel bars 5 miles above the mouth, alt. 50 ft., Tracy 9472 (♀), 9476 (♀), 9478 (♂), 9483 (♀), and 9486 (♀), all May 30, 1931 (CRB except 9478 and 9486; UC); 10811, 10816, September 24, 1932 (CRB, 10811 only; UC); shrub 1–1.5 m. high, on gravel bars in water, Parks 01054, July 10, 1931 (CRB, UC). Smith River at Gasquets, alt. 300 ft., scarce here, near its eastern limit, Tracy 10855, September 24, 1932 (CRB, UC).

Salix Tracyi Ball n. sp.

Plates 69 and 70

Sectio *Cordatae.* Frutex usque ad arbor parva 2–6 m. altus; ramulis gracilibus, minute puberulentis usque ad glabris; foliis oblanceolatis usque ad anguste obovatis, integris, tenuibus, inferne glaucis et sparse pubescentibus aut puberulentis usque ad glabris; amentis gracilibus, subpraecoquis, breviter pedunculatis, 2–4 cm. longis; squamis obovatis, obscuris, sparse pilosis; capsulis 4.5–5.5 mm. longis, glabris; pedicellis 1–2.5 mm. longis; stylis 0.2–0.4 mm. longis, integris.

A slender, graceful, sparingly cespitose, shrub or small tree, 2 to at least 6 m. high; trunks grayish-green, smooth; branchlets slender, 3-year and 2-year grayish-yellow to brownish, glabrate except behind the buds, 1-year and seasonal shoots yellowish to brown, 1-year glabrous in spring through sloughing of the puberulent epidermis, the seasonal finely puberulent or occasionally subpubescent. Bud scales stout, short, ovate or broadly lanceolate, 3–6 mm. long, mostly obtuse, colored and clothed as branchlets on which borne, color of all branchlets varying much with age and exposure.

Leaves midsize, petioled, those on vigorous shoots stipulate; stipules (on vigorous shoots only) 3–9 mm. long, 1.5–4.5 mm. wide, smaller nearly ovate, larger nearly semicordate, entire to sparingly rounded-dentate, colored as blades; petioles slender, 2–5 or 7 mm. long on fruiting branchlets, up to 1 cm. long on vigorous shoots, colored and clothed as branchlets; blades oblanceolate, elliptical-oblanceolate, or narrowly obovate, 3–5 cm. long and 1.5–1.8 cm. wide on fruiting branchlets, up to 13 cm. long and 2.5–3 cm. wide on vigorous shoots, common sizes, in cm., 4 × 1.2–1.6, 5 × 1.6–1.9, 6 × 1.3–1.5, and 7–8 × 2, or, on vigorous shoots, 10–11 × 2–2.5 and 12–13 × 2.5–3, mostly subcuneate or acute at base, those on fruiting branchlets broadly acute to obtuse or rounded and sometimes apiculate at apex and entire, those on vegetative shoots larger and proportionately narrower, acute to subacuminate, often shallowly crenate-serrulate, not or scarcely glandular, the young often puberulent or pubescent, becoming thinly so by expansion, and usually glabrate to glabrous as they become older, clear green above, glaucous beneath, midvein yellow, slender secondaries diverging at angles from 20° to 45° and curving upward near the margin, subimpressed to plane in young leaves, becoming elevated with maturity, tertiaries forming small irregular polygons.

Aments slender, midsize, subprecocious to somewhat coetaneous, on shoots of previous season; peduncles short, pubescent, bracted or leafy, staminate 2–4 mm. long and bearing 2–4 very small leaf-like bracts, pistillate 5–10 or occasionally 14 mm. long and bearing 2–4 small leaves. Flower scales spatulate-obovate or broadly oblanceolate to sometimes cuneate-oblong, 1–1.3 mm. long, entire, obtuse or truncate at apex, or lowermost sometimes acute, dark brown to blackish, thinly to rather densely clothed, especially beneath, with short grayish hairs. Gland ventral, minute or wanting.

Staminate aments 2–4 cm. long, about 1 cm. wide, yellow; stamens 2, filaments about 4 mm. long, united at base for about one-third of their length, glabrous; anthers subglobose, about 0.5 mm. in diameter.

Pistillate aments 2–5 or rarely 6 cm. long, 1.2–1.5 cm. wide, rather compact; capsules lanceolate, acute, 4.5–5.5 or 6 mm. long, usually acutish at base, long-pediceled, glabrous (ovary also), yellowish brown; pedicel slender, 1–2.5 or rarely 3 mm. long, lower always the longer, yellowish-brown, glabrous; styles short, 0.2–0.4 or 0.5 mm. long, entire; stigmas about equaling style, entire or notched; seeds oblong oblanceolate, obtuse, 1–1.2 mm. long, dark brown, coma hairs about 3 mm. long, straight, white.

Flowering occurs from late April throughout May in normal seasons and fruiting follows in due course of about two weeks.

It is a great pleasure to dedicate this species to Joseph P. Tracy, of Eureka, Humboldt County. With his sister, Miss Ethel Tracy, this veteran collector of our northern redwood paradise has done more than any other botanist to make known the flora peculiar to that area. For years he has distinguished this newly described species as the "little willow" and, as the specimens cited will show, he has collected it at many points in the two California counties.

Salix Tracyi is related most closely to *S. lasiolepis* Bentham, the abundant, widely distributed, and variable arroyo willow of California and the adjacent states. The new species differs from *lasiolepis* in its more slender branchlets; in its thinner, broader, less pubescent, more obovate, and less veiny leaves; in its smaller and much less pilose flower scales; in its smaller capsules, longer pedicels, and shorter styles; and in later flowering. The leaves of *S. lasiolepis* vary from linear or linear-oblong in New Mexico, Arizona, and southern California, to narrowly oblanceolate in most of the Coast Range area. Even the more or less obovate leaves of variety *Bigelovii* (Torrey) Bebb are thick, firm, and veiny as compared with those of *Tracyi*. In *lasiolepis* the capsules average about 5 mm. long, the pedicels seldom exceed 1 mm. in length, and the styles normally are 0.7–1 mm. long. In the same habitats and localities, *S. lasiolepis* normally flowers and fruits some two to four weeks earlier than *S. Tracyi*.

Tracy's willow is an interesting component of that group of more or less localized endemic willows of northern California and southern Oregon, which includes *S. delnortensis* Schneider, *S. Parksiana* Ball, *S. melanopsis gracilipes* Ball, and others not yet described. It occurs with *S. melanopsis*, *S. Parksiana*, and *S. Coulteri*.

Types.—The type collections of *S. Tracyi* are both from the Smith River in Del Norte County, California. The pistillate type collection is Parks and Tracy No. 0934, collected at "French Flat," just below Gasquet, on May 10, 1931. Specimens were distributed to 50 major herbariums. Tracy No. 9362 is from the same plant. The type specimen is in the Herbarium of the University of California, Sheets No. 481400 and 481401. The staminate type collection is Ball, Parks, and Tracy 01288, from Madrono Park, above Gasquet, elevation about 500 feet, on May

15, 1932. The type specimens are in the Herbarium of the University of California, sheets No. 504032 to 504035.

Distribution.—*Salix Tracyi* occurs abundantly on the numerous boulder-strewn sand and gravel bars of the rivers of northwestern California and adjacent Oregon. It has been found on the Eel, Van Duzen, Mad, Trinity, Klamath, and Smith rivers, and some of their tributary creeks in California, and on the three forks of the Illinois River and their tributary creeks in Josephine County, Oregon. It probably occurs over a much wider range in both northern California and southern Oregon but it has not yet been possible to study the material critically.

The specimens listed below have been examined. Most of them are recent collections and were distributed as *S. lasiolepis* Bentham or its variety *Bigelovii* (Torrey) Bebb. Some of these collections have been widely distributed in this country and abroad. All those collected by Mr. Tracy, and many of the others, are in his herbarium at Eureka. The following arrangement is from south to north.

California. *Humboldt County.* South Fork of Eel River between Miranda and Redway, alt. 300 ft., bush 6–8 ft. tall, along river, Joseph P. Tracy 9803 (♀), April 24, 1932 (CRB, UC). South Fork of Eel River, Sylvandale, between Miranda and Myers, Mrs. H. P. Bracelin 268, 269, May 1, 1931 (CRB, UC). Van Duzen River, Bridgeville, alt. 750 ft. shrub 10 ft. tall, on river bar, Tracy 10128 (fol.), June 4, 1932 (CRB, UC). Van Duzen River, Blue Slide, alt. 15–20 m., shrub 10–12 ft. high, on gravelly flood plain, Ball, Parks, and Tracy 01244 (♀), May 12, 1932 (CRB, UC).

Mad River, Blue Lake, alt. 15 m., small rounded tree, rare, Harold E. Parks 0997 (♀), May 20, 1931 (CRB, UC). Mad River, gravelly flood plain at Englehart gravel pit, above Blue Lake road, 2 miles east of Redwood Highway, an individual plant about 6 ft. high, forming a clump 25 ft. in diameter, Ball, Parks, and Tracy 01254 (♀), May 13, 1932 (CRB, UC, 3 sheets each). Same place, plant 3–5 ft. high, forming a clump 15 ft. in diameter, Ball, Parks, and Tracy 01255 (fol.), May 13, 1932 (CRB, UC, 2 sheets each).

Redwood Creek at Berry's (Trinity Highway from Mad River to Trinity River), Joseph P. Tracy 6189 (♂) and 6189a (♀), April 15, 1923 (UC); ——— 7154 (fol.), scraggly bush 6–10 ft. tall, June 28, 1925 (UC); ——— 7451 (♀), bush 6–8 ft. tall, May 1, 1926 (UC); ——— 7885 (♀, same bush as 7995); 7886 (♀, same plant as 7996), 6–10 ft. tall; 7887 (♀) and 7888 (♂), all April 10, 1927 (CRB 7885 and 7887; UC all); ——— 7995 (♀, same bush as 7885) and 7996 (♀, same bush as 7886), May 13, 1927 (CRB 7995 only; UC); ——— 8305, August 7, 1927 (CRB, UC). Redwood Creek at Berry's, slender shrubs 6–10 ft. high, on gravelly margin of creek, Ball, Parks, and Tracy 01319 (♀), 01320 (♀), and 01321 (♂), May 17, 1932 (CRB, UC).

Willow Creek at Graham's, about 1 mile above Trinity River, low shrub 6–8 ft. high, edge of artificial pond, Ball, Parks, and Tracy 01338 (♀), May 17, 1932 (CRB, UC). Trinity River at mouth of Willow Creek, alt. 150 m., only a single individual, 5 m. high. Parks and Tracy 0976 (♀), May 17, 1931 (CRB, UC, distributed as *S. lasiolepis bigelovii*). Hupa, Trinity River, Mrs. M. H. Manning, April-May, 1902 (UC).

CALIFORNIA. *Del Norte County.* Smith River at Roosevelt Highway Bridge, 5 miles above mouth, alt. 50 ft., gravel bars, Joseph P. Tracy 9499 (♀, low bush), 9500, 9501, and 9503 (all fol.), May 30, 1931 (UC). Smith River at Hiouchi Bridge, 8 miles below Gasquets, shrub 6 ft. high in bouldery-sandy flood plain, Ball, Parks, and Tracy 01299, May 15, 1932 (CRB, UC, 3 sheets each). Smith River ("French Flats"), just below Gasquets, alt. 300 ft. (90 m.), slender bush 10 ft. tall, Tracy 9360, May 10, 1931 (CRB, UC); slender tree, 6 m. high, Tracy 9362 (♀) and Parks and Tracy 0934 (pistillate type collection), (both from same plant), May 10, 1931 (CRB 0934 only; UC); slender, broad-leaved tree, 3–6 m. high, Parks and Tracy 0942 (fol., finely pubescent), May 10, 1931 (CRB, UC, 2 sheets each); densely branched shrub, 1–2.5 m. high, in seepage water in sandy-gravelly soil, Tracy 9363 and Parks and Tracy 0950 (♀, both from same plant), May 10, 1931 (CRB, UC); shrubs about 10 ft. high, on bouldery-sandy margin of river, Ball, Parks, and Tracy 01295 (♀), 01296 (♀), and 01298 (♀), May 15, 1932 (CRB, UC). Smith River at Madrono Park, above Gasquets, shrub about 8 feet high, in bouldery alluvium at edge of water, Ball, Parks, and Tracy 01288 (staminate type collection), 01291, May 15, 1932 (CRB, UC, several sheets of each).

Salix Farrae Ball

Plate 71

Salix Farrae Ball, in P. C. Standley, in Contr. U. S. Nat. Herb., 22:321, 1921 (Flora of Glacier National Park, Montana).

The first collections of this trim little species apparently were made by Miss Edith M. Farr at Field, in Yoho Park, southeastern British Columbia, on June 8, 1904, and June 7 and July 15, 1905. John Macoun was a close second with his specimen from near-by Emerald Lake, B. C., on August 27, 1904. Of these specimens, only Miss Farr's second collection was sufficiently complete to permit a description of the species and it accordingly became the type. It is a pleasure to dedicate the species to this able and observant collector. Her paper* on the flora of the Rocky and Selkirk Mountains of Canada was published long before this species was recognized and it is mentioned therein under *S. cordata* and *S. glaucops* (p. 30). Only with the abundant collections of N. B. Sanson from Banff and vicinity, made available in 1919 and thereafter, has it been possible to determine the range of expression in this species and to prepare a complete description of both the pistillate and the staminate plants.

The treatment given in the Flora of Glacier National Park necessarily was brief and a projected monograph of the section *Cordatae* has been prevented. It seems desirable, therefore, to present the following more complete description of the species and of some varying forms.

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* Farr, Edith M., Contributions to a Catalogue of the Flora of the Canadian Rocky Mountains and the Selkirk Range, Contrib. Bot. Lab. Univ. Pa., 3:1–88, 1 map, 1907.

Section *Cordatae.* Low shrub; branchlets reddish-brown and seasonal shoots yellowish, puberulent; leaves small, elliptical-oblanceolate to elliptical-oval, widest just above the middle, rounded at base, acute to abruptly short-acuminate at apex, entire, 1–2 cm. wide, 3.5–5 or 6 cm. long, yellowish-green, glaucous beneath, glabrous, veiny; aments small, coetaneous, on short, small-leaved peduncles, pistillate 2–3 cm., staminate 1.5–2 cm. long; scales 1 mm. long, brown, thinly pilose to glabrate; capsules 4–6 mm. long, glabrous; pedicels 1–1.5 mm. long, glabrous; styles 0.4–0.8 mm. long, entire; stigmas short; stamens 2, filaments free, glabrous.

Cespitose shrub 3 dm. to 1.5 m. high; branches ascending; branchlets ascending or somewhat divergent, more or less puberulent to glabrous, reddish brown and shining, or drying a dull reddish brown, scarcely striated; the seasonal shoots pale yellow or reddish-yellow, thinly pubescent or puberulent to glabrate; bud scales 2–4 or 6 mm. long, mostly obtuse, colored as the seasonal shoots, puberulent or glabrous or the mature bud scales pruinose (Malte and Watson 511).

Leaves small to midsized, slender-petioled; stipules wanting or occasionally 0.5–1.5 or rarely 3–6 (Sanson 2028) mm. long and semicordate; petioles slender, twisted, finely pubescent, or puberulent to glabrous, yellow or yellowish-brown; blades elliptical-oblanceolate to elliptic-oval, or broadly lanceolate (young lower ones often obovate and obtuse), usually widest just above the middle, acute to usually rounded or sometimes truncate at base, acute or on sterile twigs often abruptly short-acuminate and sometimes plicate at the apex, entire (or rarely the upper minutely glandular-serrulate), 1–1.8 cm. wide, 3–5.5 cm. long, or the largest 2.3–2.5 × 6–7.5 cm. on sterile twigs, common sizes, in cm., 1.4 × 3; 1.3 × 3.5; 1.4–1.7 × 4; 1.7–2.0 × 5, and 1.8–2.4 × 6, yellowish green and rather dull above, subglaucous to usually strongly glaucous beneath, veins above subimpressed when leaves are young but somewhat elevated in age, those on lower surface slender and becoming raised to form an open reticulation of slender veins.

Aments coetaneous, short-pedunculate; pistillate peduncles 5–10 or rarely 15 mm. long, yellow during anthesis, becoming brown, glabrous or very thinly pilose-pubescent, bearing 2–3 or rarely 4 small leaves usually 1–1.5 or 2 cm. long; staminate peduncles 3–5 mm. long, bearing 2–3 small leaves 10–12 mm. long. Pistillate aments 1–2 cm. long in anthesis, becoming 2–3 or rarely 3.5 cm. long and about 1 cm. wide in fruit; rachis glabrate to thinly pilose; scales oblong or oblanceolate, 0.7–1 mm. long, obtuse, lower portion yellowish, apical portion dark brown, sometimes completely fuscous in drying, thinly pilose beneath or becoming glabrous throughout; capsule lanceolate-acuminate, often acute at base, 4–6 mm. long, glabrous, yellowish, sometimes becoming brown in age; pedicel yellow, glabrous, 1–1.5 mm. long, or on basal capsules sometimes 1.5–2 mm.; gland short, filiform-capitate; style 0.4–0.8 mm. long; stigmas usually very short, entire or sometimes one or both somewhat bifid. Staminate ament short-pedunculate, 1.5 cm. long, slender, yellow; scales much as in pistillate flower; stamens 2, filaments glabrous, free; anthers oval or subspherical, yellow.

The staminate aments are but little known. Although many of the collections bearing only leaves probably are from staminate plants, they were made too late to obtain aments. Cusick's No. 3386*a* from the Imnaha Mountains of northeastern Oregon, collected on August 18, bears one staminate ament with full-grown leaves. This doubtless represents a second or autumnal flowering and may not be fully representative of vernal flowers. Sanson's No. 117*b* from the vicinity of Banff, Alberta, is the staminate type specimen, and part of his No. 115*a* also is staminate. It is to be hoped that collectors will be able to obtain additional staminate specimens and later to get mature foliage from the same plants.

One striking feature of most of the pistillate specimens examined is the apparently frosted condition of the aments. In a large number of these frosted specimens, the ament is distorted and all or part of the capsules are blackened. Often the rachis and pedicels show injury. In many specimens, the ovaries have not been fertilized, although this condition could result from the absence of male plants. Reproduction by seeds must be greatly reduced and possibly this is a factor in the apparently limited range of the species.

S. Farrae differs from *S. Walpolei,* its nearest relative, in puberulent, rather than pubescent branchlets, yellow rather than brown seasonal shoots, smaller and narrower leaves, shorter denser aments, acuter capsules, and longer, entire style.

Distribution.—*Salix Farrae* is a plant of wet places, chiefly swamps and marshes. It has been found sparingly in the Medicine Bow Mountains of southeastern Wyoming, the Yellowstone National Park of northwestern Wyoming, and the Wallowa and Imnaha mountains of northeastern Oregon. It occurs abundantly in the Glacier National Park of northwestern Montana, and northward along the Rocky Mountain ranges as far as Lake Louise in the Rocky Mountains Park of Alberta, and Wapta and Emerald lakes in the Yoho Park of British Columbia. This carries it north nearly to latitude 51° 30′. Very probably its known range will be extended as more collecting is done in the northern mountains. It occurs at relatively high altitudes, varying from 7000 or 8000 feet in the southern portion of its ranges to 5000 or 6000 feet in Glacier Park and 4000 to 5000 in the Canadian Mountains. Its zonal distribution is upper Transition and Canadian. The following specimens have been studied. The geographic arrangement is from east and south to west and north.

WYOMING. *Albany County.* Open parks, Nash's Fork, Medicine Bow Mountains, A. Nelson 7824, July 30, 1900 (UC). Yellowstone National Park, Obsidian Creek, in small clumps 2–6 ft. high, A. and E. Nelson 6098 (CRB); on a boggy slope, 3–4 feet high, A. and E. Nelson, 6104 (Mus. Paris, USN), both July 24, 1899; upright shrub, on exposed hillsides, Upper Reynolds Creek, elev. 5300 ft., Bassett Maguire 474, July 20, 1932 (UAC).

MONTANA. *Glacier National Park.* Along Apekunny Creek, 2–3 ft. high, in open mossy bog, P. C. Standley 16930, August 2, 1919 (CRB, USN). Vicinity of Cracker Lake, alt. 1740 to 1920 m., common, on rock slides above lake, Standley 15755 (USN); moist place at foot of cliff, 3 feet high, 15813 (CRB, USN), July 15, 1919. Vicinity of Grinnell

Glacier, alt. 1650–1950 m., 2–4 feet high, common on rocks near brook, Standley 16753 (CRB, USN), July 31, 1919. Vicinity of Grinnell Lake, alt. 1500–1650 m., in marsh, 3 feet high, Standley 16109, 16110, July 21, 1919 (CRB, USN). Along Swiftcurrent Creek, below Lake McDermott, alt. about 1350 m., 1–2 feet high, abundant in open marsh, Standley 16058, July 20, 1919 (CRB, USN).

OREGON. *Wallowa County.* Shrub 3–5 feet high, on the Imnaha River, alt. 7000 ft., W. C. Cusick 3386, 3386*a*, August 18, 1909 (CRB as *S. monticola* Bebb; USN, on sheet 622467 as a mixture with Cusick 3383, *S. melanopsis*). Wet, higher Wallowa Mountains, near the lake, a low shrub, W. C. Cusick 2302 (as *S. commutata denudata*), August 2, 1899 (USN, four small immature twigs, 3 pistillate and 1 staminate, probably all belonging to *Farrae,* and, if so, one pistillate twig representing variety *microserrulata* Ball).

ALBERTA. Margins of streams, Oldman River, W. Dawson 24334 (as *S. cordata*), August 7, 1883 (NMC). *Rocky Mountains Park.* Elbow River, J. Macoun 41, June 23, 1897 (CRB, NMC, 94441, as *S. lutea*). Lake back of Mount Assiniboine (20 mi. S.W. of Banff), N. B. Sanson 811, 813, 816, August 26, 1921 (CRB, RMP). Banff and vicinity: swampy ground to Calumet Camp, Banff, Sanson 603, July 29, 1924 (CRB, RMP); Museum Grounds, back of cages, Sanson 95, 132, 134, 180, June 9, 10, 19, 21, 1911 (CRB, RMP). By the Spray River, Sanson 108, June 9, 1911 (CRB, RMP, pedicels up to 2 mm. long). Damp places, Cave Avenue, Macoun 24337, June 26, 1891 (NMC, as *S. cordata* var.). River Avenue, Sanson 336, August 2, 1911, and 2032, August 12, 1911 (CRB, RMP). Cascade Mountain (about 5 miles north of Banff), 2028, and 2207 (Cascade Camp), August 26, 1916 (CRB, RMP), and 2027 (amphitheater), September 2, 1916 (CRB, RMP). Side of 40-mile Creek, Sanson 2048, June 13, 1900 (CRB, NMC 25358 as *S. cordata,* RMP). Without specific locality, Sanson 228, June 29, 1911 (CRB, RMP), 241, 315, 317, 318, and 322, all July, 1911 (CRB, RMP), 338, 359, 386 (smaller, obovate leaves), 390, 415, 440, 2034, all August, 1911 (CRB, RMP). Mud Lake, 12 miles out (from Banff), on way from Spray Lake to Kananaskis Lake, Sanson 115*a,* 117*b* (staminate), June 30, 1928 (CRB). Palliser Pass, alt. about 7000 ft., Sanson 503, July 29, 1922 (CRB). Castlemount Ranger Station, in swamp about 3 miles east, alt. 4300 ft., Malte and Watson 508, 511 (ovate-obovate leaves), 513, June 21, September 4, 1925 (CRB, NMC, 116774, 116777, 116779; UC). Upper end of Lake Louise, alt. 5700 ft., Malte and Watson 1081, July 9, 1925 (CRB, NMC, 116813); 2–4 ft. high, near chateau at Lake Louise, J. G. Jack 2927, as *S. Barclayi,* September 18, 1922 (AA). Moraine Lake, W. A. and C. B. Setchell, August 8, 1923 (UC). *Nordegg District.* In spagnum muskeg, near Sunbeam Cabin, Nordegg River, A. H. Brinkman 3733, July 28, 1928 (CRB).

BRITISH COLUMBIA. *Yoho Park.* Emerald Lake, J. Macoun 68901, as *S. cordata* var., August 21, 1904 (CRB, NMC). Field, along the Kicking Horse River, on the flats which are often overflowed in July, when snows melt, Edith M. Farr 558, June 7, July 15, 1905 (CRB, pistillate type) and Edith M. Farr (as a mixture with *S. glauca glabrescens*), June 8, 1904 (CRB). North side of Wapta Lake, J. Macoun 68900, *S. cordata* var., August 2, 1904 (CRB, NMC). Burgess Pass trail, alt. 6500 ft., shrub 3 ft. high, Titus Ulke, July 28, 1922 (Ulke).

S. Farrae microserrulata n. var.

Marginibus foliorum serrulatis aut crenulato-serrulatis.

This variety differs from the species in having the margins of the leaves shallowly but not always regularly serrulate, or sometimes crenulate-serrulate. The blades tend to be a little narrower than in the species.

On many shoots of typical *Farrae* the apical leaf or leaves may be somewhat serrulate. This is true also of the apical leaves of some other species with normally entire margins, as *S. planifolia* Pursh. Occasionally, however, a specimen has all or nearly all its leaves with the margins finely and regularly serrulate. Such specimens do not seem to differ in other respects from typical *Farrae,* though this is not wholly certain. The majority of such specimens are without fruit or have only unfertilized capsules. It seems desirable to designate these as a variety of the species because the consistent serrulation changes the aspect of the leaf materially and requires recognition in the keys. The following specimens are placed here.

ALBERTA. *Rocky Mountains Park.* Banff and vicinity, springy thickets, Sundance Canyon, near Banff, alt. 4500 ft., M. O. Malte and W. R. Watson 898, July 4, 1925 (CRB, pistillate type; NMC, 116806); swamp, Canyon Road, N. B. Sanson 1 x, August 21, 1911 (CRB, RMP); without specific locality, N. B. Sanson 270, July 8, 1911 (as *S. pseudo-monticola*), 327, July 27, 1911, 328 (capsules to 7 mm. long), July 28, 1911, 340, August 3, 1911, 395, August 16, 1911, and 2040, August 10, 1911 (all CRB, RMP).

Salix Setchelliana n. sp.

Plate 72

Sectio *Herbaceae* (*Retusae*). Frutex prostratus aut decumbens sparse ramosus; ramulis gracilibus, paucifoliosis, juvenis albo-hirsutis; foliorum laminis anguste usque ad late oblanceolatis, 2–6 cm. longis, basi cuneatis, apice acutis usque ad retusis, irregulariter glanduloso-crenulato-serrulatis; amentis coetaneis, 1.5–2 cm. longis, folioso-pedunculatis; squamulae florum obovatis, 3–4 mm. longis, plerumque retusis, pallide luteis, glabris; staminibus 2, filamentis liberis, basi sparse pilosis; capsulis lanceolatis, 6–7 mm. longis, subsessilibus, glabris; stylis stigmatibusque 0.2–0.3 mm. longis.

Prostrate or decumbent sparingly branched shrub, branches slender, 2–5 cm. long, 0.5–2 mm. in diameter, usually more or less tortuous, older glabrate and sometimes subglaucescent, younger white-hirsute, or late seasonal shoots glabrate; bud scales inconspicuous, 2–4 mm. long, densely white-hirsute.

Leaves exstipulate, scarcely petioled; stipules wanting (in specimens seen); petioles obsolete to 1–2 or rarely 3 mm. long, broad, stout, channeled above, almost clasping, broadening imperceptibly into the cuneate base of the blade, yellow, glabrous, or sometimes more or less white-hirsute; blades small, 3–5 or rarely 6 to a branchlet, mostly narrowly to broadly oblanceolate with cuneate base tapering imperceptibly into short or almost obsolete petioles, lower and smaller sometimes elliptical-oblanceolate or obovate and less cuneate at base, narrow apical ones acute, others rounded or shallowly to deeply emarginate to retuse at apex, 1.5–5 or 6 cm. long, 0.8–1.5 or 1.8 cm. wide, common sizes, in cm., 1.5 × 0.6–0.8, 2 × 0.9–1, 2.5 × 1.5, 3 × 1.1–1.5, 3.5 × 0.8, 3.5 × 1.1–1.4, 4–4.5 × 1, 4 × 1.3–1.7, 4.5 × 1.5, 5 × 1, 5 × 1.8, 5.5 × 1.7, and 6 × 1.2, thick, firm, chartaceous, margins irregularly and remotely to rather closely, shallowly to rather deeply glandular-crenulate-serrulate, veins diverging at angles of from 20° to 40° and straightish in their lower portions, curving inward gently toward apex, mostly plane, yellowish-green and glabrous above, and more or less white-hirsute while unfolding, paler, somewhat glaucescent, and glabrous beneath in age, or the hairs more or less persistent on the midrib and primary veins.

Aments coetaneous, 1.5–2 cm. long, mostly 12- to 18-flowered, terminating short (0.5–1.5 or 2 cm. long) white-hirsute to finally glabrate or glabrous seasonal branchlets bearing 2–3 normal leaves; flower scales broadly oblanceolate, obovate, or obconic, often appearing oblong in pressed specimens because the margins become infolded around the stamens, rounded to truncate or commonly retuse or bicuspidate at apex, 3–4 or 4.5 mm. long, finely striate with sometimes branching veins, persistent, glabrous, pale yellow or straw color.

Staminate aments slender, 1.5–2 cm. long, yellow; stamens 2, filaments little exceeding the scales, free, thinly pilose on the lower one-fourth to one-third; anthers oblong, drying linear, and superficially resembling stigmas when protruding from beneath the elongated scales; pistillate aments oblong to broadly oblong; capsules broadly lanceolate, 6–7 or 7.5 mm. long, bluntish at apex, rounded at base, subsessile, thick, brown, glabrous; pedicel stout, 0.1–0.2 mm. long; style (from over-mature specimens) stout, 0.2–0.3 mm. long; stigmas apparently as short; gland 1, ventral, slender, 0.8–1 mm. long, somewhat capitate.

It is both a pleasure and an honor to dedicate this unusual species to Professor William A. Setchell, of the Department of Botany, University of California, and his charming wife, Mrs. Clara B. Setchell. Their extensive, arduous, and discriminating collecting of more than 670 numbers of willows in Alaska and adjacent portions of British Columbia and Yukon Territory in 1931 and 1932 has made possible an adequate treatment of the genus as it occurs in that region. Already through study thus made possible, several species and varieties have been added to the known flora and the botanical world has been placed under a large debt of appreciation.

To Mrs. Ynes Mexia belongs the credit for the first discovery of this species, in 1928. The collection consisted of pistillate material long past maturity of the fruit. It was not possible to delimit the species until the collection of abundant staminate material by Dr. and Mrs. Setchell and of equally abundant pistillate material in somewhat better condition for study, by Mr. David Kaye, at Dr. Setchell's request.

Salix Setchelliana is abundantly distinguished from any other American species of the *Herbaceae-Retusae* group. The large leaves, from 2 to 6 cm. long, with the margins more or less irregularly and shallowly glandular-crenulate-serrulate, differ completely from the small leaves of the other species, which are usually from 5–15 mm. wide and rarely exceeding 2 cm. in length. Those of *polaris, phlebophylla,* and *rotundifolia* are entire, while those of *herbacea* and *uva-ursi* are finely and evenly crenulate. The large (3–4 mm. long) yellowish and glabrous flower scales also are distinctive. Of the Old World species of the section, it probably is most closely related to *S. retusa* L., from which it differs in the much larger leaves, with glandular-crenulate margins.

Distribution.—*Salix Setchelliana* is known at present only from Mount McKinley National Park in central Alaska, and from the district between Lake Kluane and the Don Jek River on the east side of the St. Elias Range in southwestern Yukon Territory. It seems probable that it will be found to be distributed more widely in the mountains or northwestern North America. The type locality is the snout of the Muldrow Glacier at the base of Mount Eielsen in Mount McKinley National Park, Alaska.

The specimens which have been examined are listed below. Mexia No. 2095 has been distributed to some eighteen of the leading herbariums of the United States and Europe. Specimens are listed below only for those in which the writer has seen the material. Specimens of the type collections, pistillate and staminate, will be distributed presently to about twenty-five of the leading herbariums of the world. The writer personally has examined all the specimens but cannot list these herbariums because the distribution has not yet been completed.

YUKON TERRITORY. Lake Kluane to Don Jek River (southwestern Yukon, on east side of St. Elias Range), Adolf Müller, August 11–27, 1920 (PANS, distributed as *Salix Farrae?*).

ALASKA. *Mount McKinley National Park, central Alaska.* Shrub on gravel bar in river bed, near foot of Copper Mountain, Thoroughfare Pass, alt. 1000 m., Mrs. Ynes Mexia 2095, July 12, 1928 (CRB, PANS, UC; distributed unnamed; post-mature fruit). Low or prostrate shrub scattered in moist gravel of an area 30–40 ft. in diameter at snout of Muldrow Glacier, opposite ranger cabin ("Copper Mtn. Camp"), base of Mt. Eielsen, elev. about 3000 ft., William A. and Clara B. Setchell 587 (staminate type collection), July 12, 1932 (CRB, UC; type specimen, sheets Nos. 486279 and 504076, just past flowering); same place, David Kaye 1 (pistillate type collection), about August 31, 1932 (CRB; UC, type specimen, sheets Nos. 504077–504078).

Salix brachycarpa var. Mexiae n. var.

Plate 73

Sectio *Glaucae.* Pedunculis 1–2.5 cm. longis; amentis elongatis, laxis, circa 20-floriis, staminatis 1–2 cm. longis, pistillatis 2–3.5 cm. longis; a forma typica per et pedunculos longiores et amenta longiora laxioraque abludens.

Prostrate or spreading shrub, 3–5 or 7 dm. high; older stems dark gray or brownish gray, roughened with bud scars, branching freely at top of stem; the branchlets mostly divaricate, sometimes ascending, very leafy, the free apical branching and leafiness giving a top-heavy aspect to specimens; 2-year and 1-year shoots dark brown, full of leaf scars, sparsely or 1-year more densely pilose-pubescent, seasonal shoots more or less densely white-pilose; bud scales short, oval, about 2 mm. long, obtuse, chestnut or yellowish-brown, pilose-pubescent or becoming glabrate.

Leaves small, short-petioled, rarely stipulate; stipules wanting or minute, up to 2 or 3 mm. long on vigorous shoots, lanceolate, acute, pilose; petioles stoutish, 2 or sometimes 3 mm. long, pubescent; blades small, mostly elliptical, or elliptic-oblong, sometimes elliptic-lanceolate or elliptic-oblanceolate, 2–3.5 or 4 cm. long, 7–10 or 14 mm. wide, common sizes 20 × 8, 25–30 × 7–10, 30–40 × 7–14, and 35 × 12 mm., obtusish (the broader) to acute or abruptly acute at the apex, usually rounded but sometimes somewhat narrowed at base, often minutely and rather remotely glandular-denticulate on lower portion of the margin, yellow midrib and primary veins usually prominent beneath and sometimes raised on upper surface, cross veinlets often forming a fine reticulation beneath, and occasionally above, yellowish green above, glaucescent to densely glaucous beneath, the young soft-pilose with white hairs on both surfaces, becoming glabrate to glabrous with maturity, especially beneath, but margins always permanently ciliate.

Aments coetaneous or subserotinous, leafy-pedunculate, lax; peduncles relatively long, slender, pilose-pubescent, the staminate 1–1.5 cm. long, the pistillate 1.5–2.5 cm. long, both bearing 3–6, usually 4, leaves; scales obovate-oblong when expanding, becoming narrowly oblong or oblanceolate, obtuse, 1.5–2 mm. long, pilose, yellowish throughout or darkened at tips, sometimes brownish throughout; pistillate aments oblong, 2–3.5 cm. long, 1.2 cm. wide, lax, about 20-flowered; capsules narrowly lanceolate, 6–7 mm. long, subsessile or the lowermost distinctly pediceled, the ovaries white-pilose, mature capsules yellowish, thinly pilose; pedicels nearly obsolete or those of lower capsules up to 0.5 mm. long, stoutish, pubescent; styles mostly entire or occasionally divided at apex, 0.7–1 mm. long; stigmas usually divided, about as long as styles; staminate aments 1–1.8 cm. long, lax, oblong; stamens 2, filaments free, glabrous or sparingly pilose at base for one-fourth to one-third of length.

Variety *Mexiae* differs from the typical species chiefly in the longer peduncles, 1–2.5 cm. long; the elongated, lax, oblong aments, the pistillate 2–3.5 cm. long in fruit and about 20-flowered; the staminate 1–2 cm. long, lax, oblong.

This probably is the plant mentioned by Schneider (Bot. Gaz., 66: 337, 1918) in his discussion of *S. brachycarpa* Nuttall, in the following words:

> An uncertain form is represented by no. 74. Hb. H.B. and T. (fr.; N.), named *S. desertorum* var. *acutifolia.* It differs from the type by foliis subacutis ad 32:9 mm. magnis et praecipue amentis fructiferis satis laxifloris ad 3.5:1 cm. magnis.

Distribution.—*Salix brachycarpa* was not known to occur in Alaska when Coville monographed the willows of the Territory in 1901. The material in hand at the present time indicates a limited range, though future exploration may greatly broaden it. The following collections have been examined.

British Columbia. *Lake Atlin District.* Shrub, 2–3 ft. high, edge of hydromagnesite swamp, Atlin, W. A. Setchell and H. E. Parks 11 (staminate and pistillate), July 10, 1930 (CRB, UC, 2 sheets, too young for certain determination); Mount Monarch, near Atlin, Setchell and Parks 12, July 11, 1930 (CRB, UC); Warm Springs, 20 miles south of Atlin, Setchell and Parks 13, July 9, 1930 (UC).

Yukon Territory. *Carcross* (near Lake Bennett), Alice Eastwood 722 (staminate), July 16, 1914 (CAS, USN; apparently about 3 dm. high, branchlets and leaves glabrate, peduncles less than 1 cm. long, CRB); 723 (pistillate), July 16, 1914 (CAS, USN; branchlets and leaves glabrous except for ciliate leaf margins, peduncles 1 cm. or less, aments dense but laxer at base; both distributed unnamed). *Cowley,* Yukon River, elev. approx. 2400 ft., W. A. and C. B. Setchell 323 (too immature for certainty) and 330, June 14, 1932 (CRB, UC). *Dawson.* Dawson Slide, Alice Eastwood 81 (May 19), 161 (June 7), 1914 (CAS, distributed unnamed; apparently a low and much-branched plant, leaves very small, 8–18 mm., glabrous except the ciliate margins, peduncles less than 1 cm. long but not yet fully developed).

Alaska. *McKinley National Park.* Prostrate shrub, up to 30 cm. high, forming dense thickets, rock (moraine)-covered snout of Muldrow Glacier, alt. 1000 m., Ynes Mexia 2131 (pistillate type collection; CAS, CRB; UC, type sheets Nos. 384376, 441340, and 441341; USN), 2132 (staminate type collection), July 23, 1928 (CAS, UC, type sheet No. 384375, distributed as *S. niphoclada* Rydberg); spreading shrub, 7.5 dm. high, on gravel bar in McKinley River, on trail from Wonder Lake to McKinley Bar, near center of north boundary of Park, alt. 700 m., Ynes Mexia 2270 (pistillate), August 22, 1928 (CAS, UC, distributed unnamed); spreading shrub, 30 cm. high, on rock slide, on precipitous slope above camp, Toclat River, at upper edge of brush line, alt. 800 m., Ynes Mexia 2282 (pistillate), August 23, 1928 (CAS, PANS, UC, distributed as *S. glauca*); spreading shrub, up to 7.6 dm. high, open spaces in spruce woods on flat north of Savage Camp (on Savage River), alt. 900 m., Ynes Mexia 2083 (pistillate), 2084 (staminate), July 6, 1928 (CAS, CRB, PANS, UC, USN, both distributed as *S. glauca*); Savage River Camp, elev. 2650–2700 ft., W. A. and C. B. Setchell 159, June 28, 1931 (UC). Yukon River, Fort Yukon, moist road in open spruce-aspen woods, L. F. Henderson 15045, 15046, August 7, 1932 (CRB).

Salix brachycarpa var. **Sansoni** n. var.

Sectio *Glaucae.* A forma typica per folia breviora latioraque, late elliptica usque ad ovata et apice acuta, aut occasione oblata obovata et apice obtusa, 10–20 mm. usque ad 25 mm. longa, 5–9 mm. usque ad 12 mm. lata abludens.

Low, erect or ascending shrub, 2–5 or 7 dm. high; bark reddish brown; branchlets numerous, epidermis peeling off in papery flakes, those of the season pubescent; buds ovate, obtuse, 1 mm. long, pubescent; leaves small; petioles scarcely exceeding 1 mm.; blades mostly broadly elliptical or ovate and acute at apex, occasionally obovate and obtuse at apex, rounded at base, entire, 5–9 or 12 mm. wide, 10–20 or 25 mm. long, at first distinctly villose-tomentose with yellowish hairs, becoming glabrous and somewhat shining above and somewhat glabrescent and glaucescent beneath, veins raised on both surfaces but more distinctly so above.

Aments small, globular, about 1 cm. in diameter, subsessile, bracteate, 12–15- or 20-flowered; capsules subsessile, 4–5 or 6 mm. long, obtuse, softly yellowish-tomentose; style about .7 mm. long, stigmas notched; stamens 2, filaments pubescent at base.

Variety *Sansoni* differs from the species chiefly in the smaller size of the plant and all its parts, especially in the shorter and relatively broader leaf blades, and the subsessile, nearly globular aments. The elliptic-ovate or obovate blades, 1–2 cm. long, contrast with the mostly oblong to broadly elliptical blades, 2–5 cm. long, and the subsessile roundish aments contrast with the plainly peduncled and elongated aments, of the species.

It is a pleasure to associate with this little northern willow the name of Mr. N. B. Sanson, long-time curator of the Government Museum in the Rocky Mountains National Park, Banff, Alberta, Canada. His tireless energy and enthusiasm have made the flora of that most interesting district much better known than formerly. The type collection was made by him in British Columbia, as listed in the specimens examined, and he has made other collections in the adjacent portion of Alberta, around Banff.

Distribution.—This variety occurs sporadically in extreme northeastern Oregon, is fairly common in the Rocky Mountains Park of southwestern Alberta, apparently less common in the adjoining mountainous area of British Columbia, and reappears in the Gaspé district of eastern Quebec, which has been so well explored and described by Fernald. The species ranges from Colorado and Utah northward in the Rocky Mountains to the Mackenzie River, and eastward to Hudson Bay. In the far north, Yukon and Alaska, it is represented by variety *Mexiae.*

The following specimens have been examined.

OREGON. *Wallowa Mountains.* On mountain sides near the lake, 8000 ft. alt., Wm C. Cusick 2298, July 31, 1899 (UC).

BRITISH COLUMBIA. North side of Wapta Lake, John Macoun 68887, August 2, 1904 (CRB, NMC). Starbird Glacier Valley, Lake of the Hanging Glacier, Windermere District, N. B. Sanson 118 (CRB, RMP) and 119 (CRB, RMP, UC), both July, 1928. No. 119 is the type collection, containing both male and female plants, the latter being the specific type. The specimens in the herbarium of C. R. Ball are the type specimens.

ALBERTA. Rocky Mountains Park, Banff, N. B. Sanson 375, August 11, 1911 (CRB, RMP); Sanson 389, August 15, 1911 (CRB, RMP); M. O. Malte 122183, 122190, July 9, 1918 (NMC, UC). In muskeg, Mercoal, near Coalspur, alt. 4300 ft., Malte and Watson 116891, 116893, August 8, 1925 (NMC, UC).

QUEBEC. Wet serpentine barrens, alt. about 1060 m., tableland of Mount Albert, Gaspé County, Fernald, Griscom, Mackenzie, and Smith 25663 (CRB, GH), July 24, 1923. (The leaf blades of this specimen are much more densely tomentose than are those of the western plants.) The sheet of No. 25667 in the herbarium of University of California, collected by the same persons at the same time and place, bears one ample specimen of the species and one 10-cm. branchlet of this variety (UC).

Salix glauca var. **Aliceae** n. var.

Plate 74

Salix glauca acutifolia (Hooker) Schneider (in part), Schneider in Bot. Gaz. 66: 326–329, 1918; *ibid.*, 67:60–62, 1919; Schneider in Jour. Arnold Arb. 3:114, 1921.

Sectio *Glaucae.* A forma typica per folia elliptico-oblonga usque ad ovata, oblongo-ovalia, aut obovata, basi late rotundata, usque ad interdum subcordata (sed nunquam cuneata) abludens; pedicellis capsularum longioribus, 1–1.5 mm. longis; stylis plerumque integris.

Branchlets more or less, often densely, white-villous, those of the season usually densely white-villous, the 1-year less so; stipules usually broader than in the species, 4–5 x 2–3, or 8 x 4 mm., or the larger 20 x 10 mm., somewhat semicordate and dentate near the base, mostly pilose; petioles 5–8 mm., or up to 12 mm. on seasonal shoots, pilose to villous; blades elliptic-oblong to oval, oblong-oval, or obovate, base broadly cuneate while developing to mostly broadly rounded or occasionally subcordate to cordate, apex acutish to abruptly acute to obtuse, 3.5–5 x 1.5–2, up to 5–6 or 7 x 2.5–3 or 3.3 cm., more or less pilose on both surfaces, never becoming glabrate.

Aments inclined to be dense, 2–6 cm. long; scales as in the species but usually more densely white-villous; filaments glabrous or sparsely pilose at base, free or united for one-half to one-third their length; capsules more elongated, 8–10 mm. long, usually densely white- or gray-villous or tomentose; pedicel longer, 1–1.5 mm. long; styles entire or rarely the apex divided, about 1 mm. long; stigmas divided, 0.6–0.8 mm. long.

This variety inclines toward *S. cordifolia* in the broader and sometimes subcordate bases of the leaves, in the longer capsules (8–10 mm.), and in the usually undivided styles. It differs from *glauca* in these three characters and in the usually broader stipules. Its relationship to *S. glauca* is shown by the erect habit, the usually stout and straight branchlets, the large stipules and leaves, and the long stout aments, as well as by the rather copious long white hairs on the branchlets.

Schneider (Bot. Gaz. 67:61, 1919) has described a *forma poliophylla* of the variety, *S. glauca acutifolia* (Hooker) Schneider. He cites under it only the type specimen, Preble and Preble 139 (cited below), and states that six other collections from the Slave Lake district of Mackenzie Territory, namely, Preble and Preble 141, and E. A. Preble 194, 196, 198, 330, and 332, look intermediate between his new form and the variety *acutifolia.* He suggests also (p. 62) that on further investigation these plants might prove to be a new form "more closely related to *cordifolia.*" The plant, however, seems to be closely connected with *S. glauca,* from which it differs in more measurable characters than hairiness.

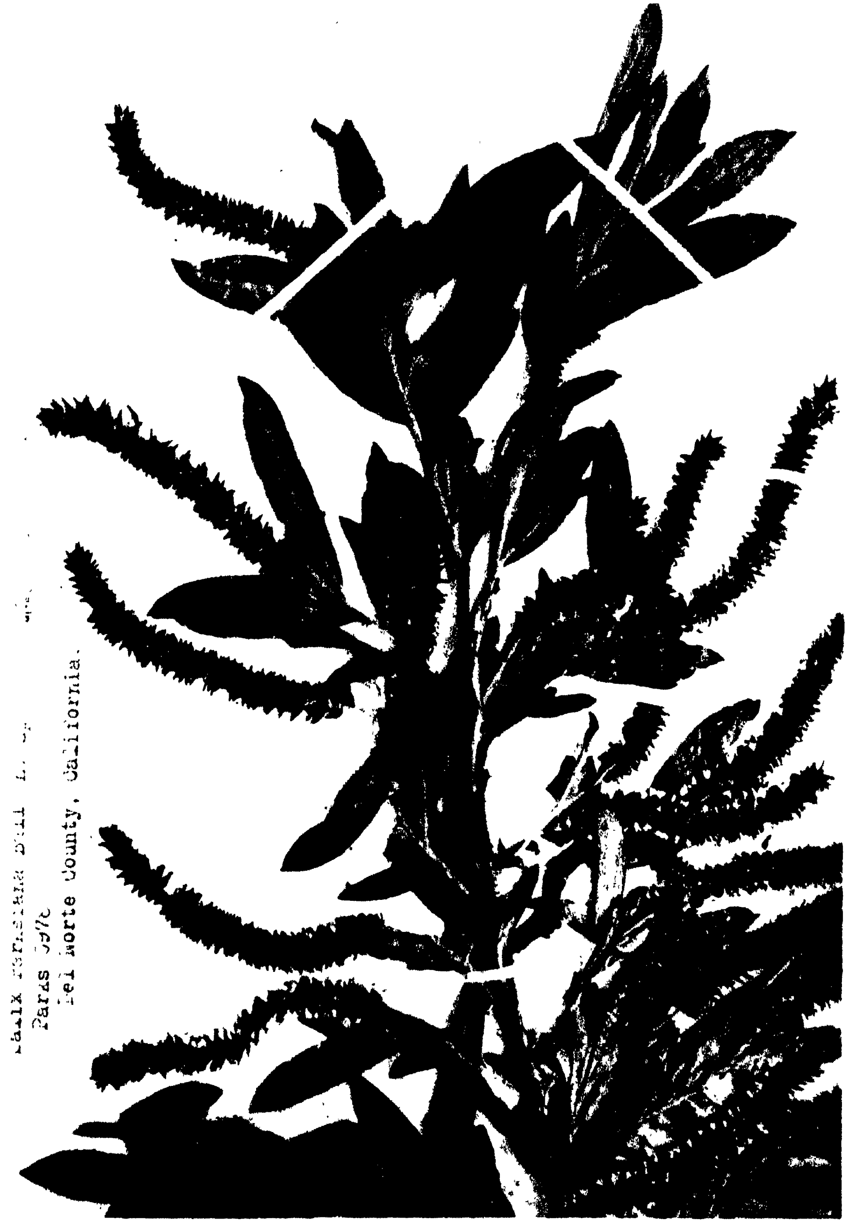
Distribution.—The variety seems to be confined to the eastern part of the range of *glauca* in North America. The specimens cited below come mostly from the upper Yukon Valley in Yukon Territory and the upper Mackenzie Valley in the district about Great Slave Lake. It is difficult to separate it with certainty from *glauca* when the leaves are just expanding. It is probable, therefore, that some of the specimens listed as *S. glauca* really represent this variety in stages too juvenile for certain determination.

MACKENZIE TERRITORY. *Fort Resolution.* Edward A. and Alfred E. Preble 141, July 4, 1901 (USN, branchlets densely pilose-hirsute; leaves oblong, the upper subcordate at base); E. A. Preble 194, 196, 198, June 21, 1903 (USN, 194 immature, the others juvenile; Rydberg has annotated all three: "Near *S. niphoclada* Rydberg, but with much broader and shorter leaves, fide P. A. Rydberg"). *Fort Good Hope.* E. A. Preble 330, 332, July 23, 1903 (USN, juvenile; determined as "*S. niphoclada* Rydberg, fide P. A. Rydberg").

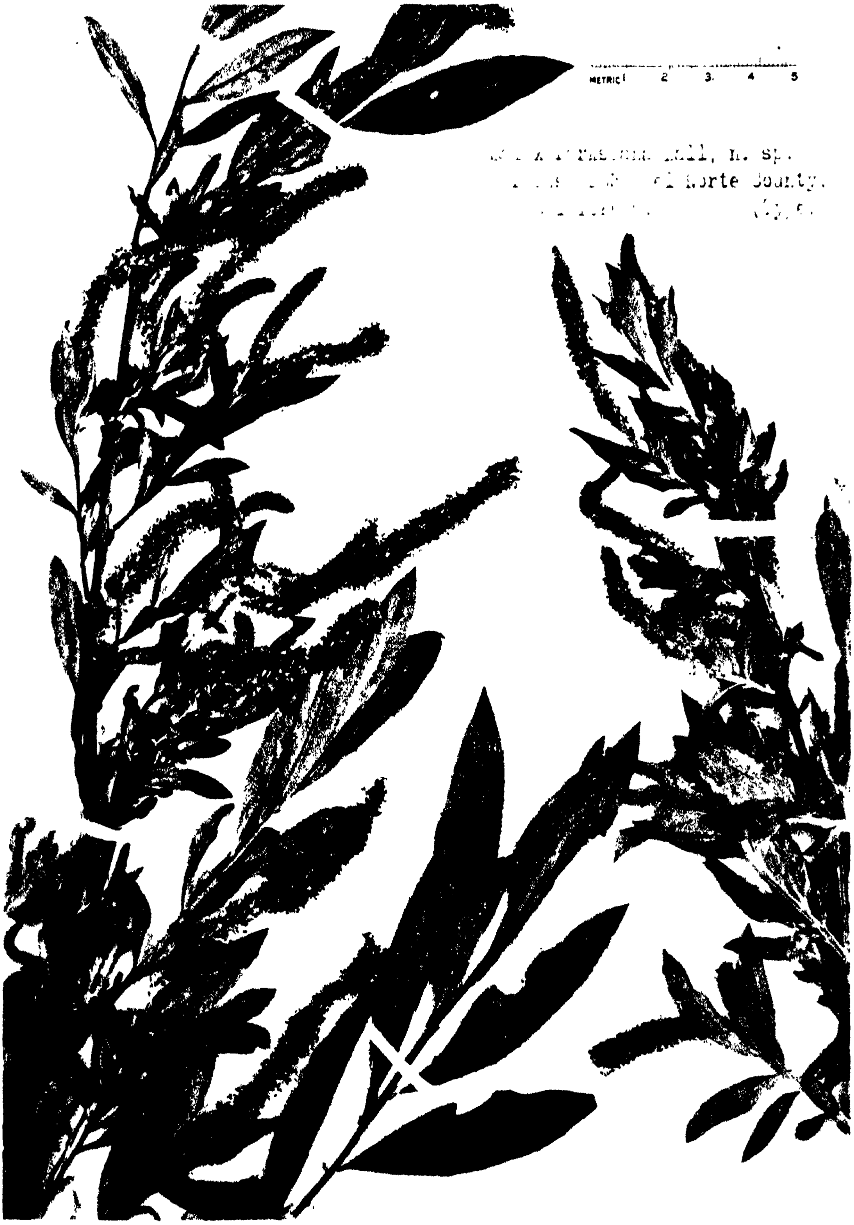
YUKON TERRITORY. *Yukon Valley.* Whitehorse, Alice Eastwood 614 (type), July 12, 1914 (CAS, pistillate type; USN) and August Kusche, May, 1916 (CAS, 2 sheets, staminate type); common, R. S. Kellogg, July 14, 1909 (USN, fruit). Flats around Whitehorse, elev. about 2100 ft., W. A. and C. B. Setchell 336, June 15, 1932 (CRB, UC). Bush 5 ft. high, along W. P. & Y. Ry., 16 miles south of Whitehorse, elev. 2700 ft., R. S. Kellogg, July 13, 1909 (USN, fruit). Shrubs 2–2.5 ft. high, decumbent at base, on right bank at Tantalus Coal Mines, near Carmacks, elev. about 1600 ft., W. A. and C. B. Setchell 368, 368a, June 16, 1932 (CRB, UC). Tall sprangly shrub on left bank 6 miles below Selkirk, alt. about 1300 or 1400 ft., W. A. and C. B. Setchell 370, June 16, 1932 (CRB, UC). Bank of Little Salmon River, shrub 8 ft. high, Victor Duran 2038, July 4, 1928 (CRB). Hard-luck Slough, Alice Eastwood 558, July 10, 1914 (CAS, USN, fruit). On island 20 miles below Dawson, Arthur J. Collier 1, June 16, 1902 (USN, leaves immature, tending to be broader and more obovate). Dawson, Alice Eastwood 504, July 2, 1914 (CAS, 2 sheets; USN, vigorous seasonal shoots, with large, broadly elliptical-ovate or subovate leaves), Dawson, elev. 1000–900 ft., W. A. and C. B. Setchell, 377, June 17, 1932 (CRB, UC), Dawson, M. O. Malte 122158, August 7, 1916 (UC). 24-Miles House, Alice Eastwood 386, June 25, 1914 (CAS, USN; young leaves narrow but broad-based, filaments united for one-half or one-third their length, glabrous). Hootalinqua, Lewes River, R. S. Kellogg, July 16, 1909 (USN, shoots thinly pilose; leaves mature, broad and short, elliptic-obovate, acute or obtuse).

ALASKA. *Central District.* Mount McKinley National Park, Sable Pass, elev. 3700 ft., W. A. and C. B. Setchell 179, June 29, 1931 (CRB, UC, immature and identification not certain). Healy, elev. 1369 ft., W. A. and C. B. Setchell 150, June 28, 1931 (CRB, UC). *West-Central District.* Norton Sound, Stuart Island, south side near Chilnit Bluff, Charles H. Rouse 24, July 29, 1931 (CRB).

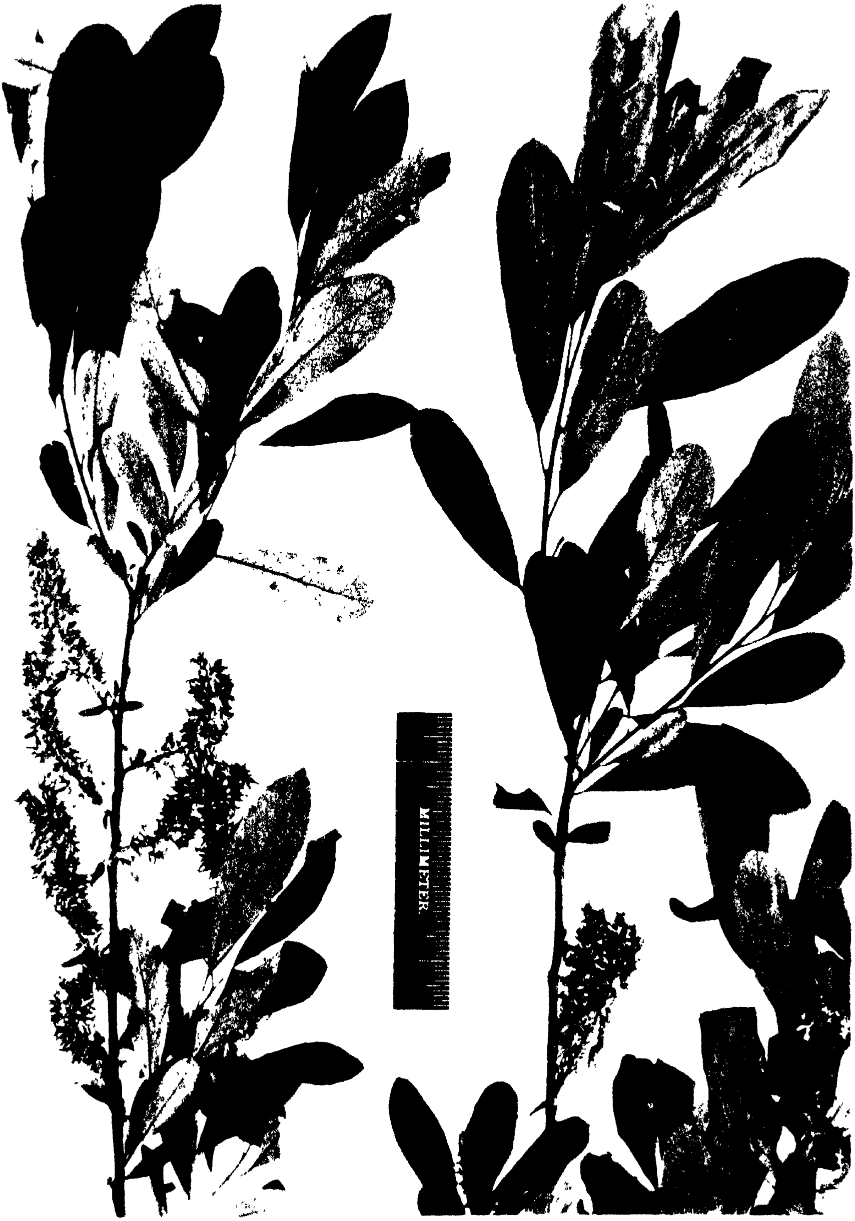
PLATES



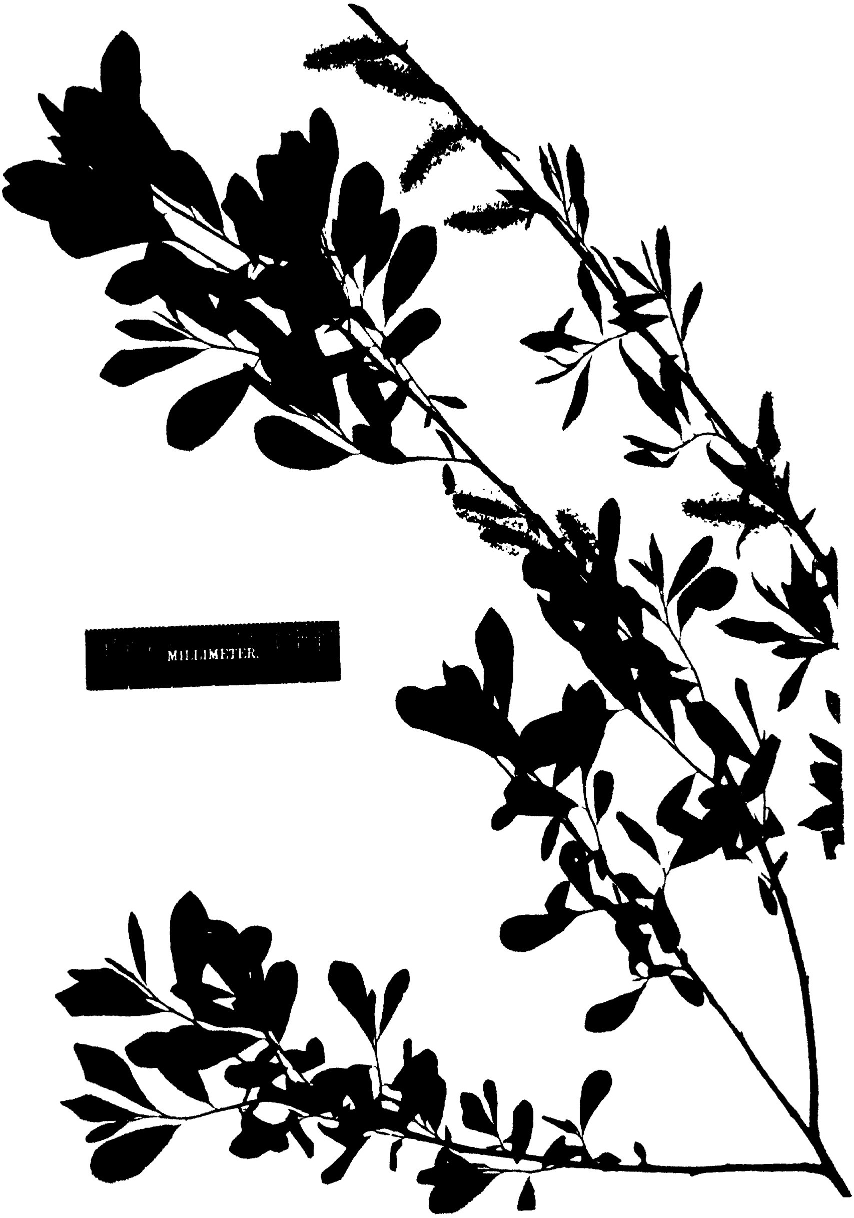
Salix Parksiana Ball. Fruiting branchlet with leaves nearly full-grown. × 3/4



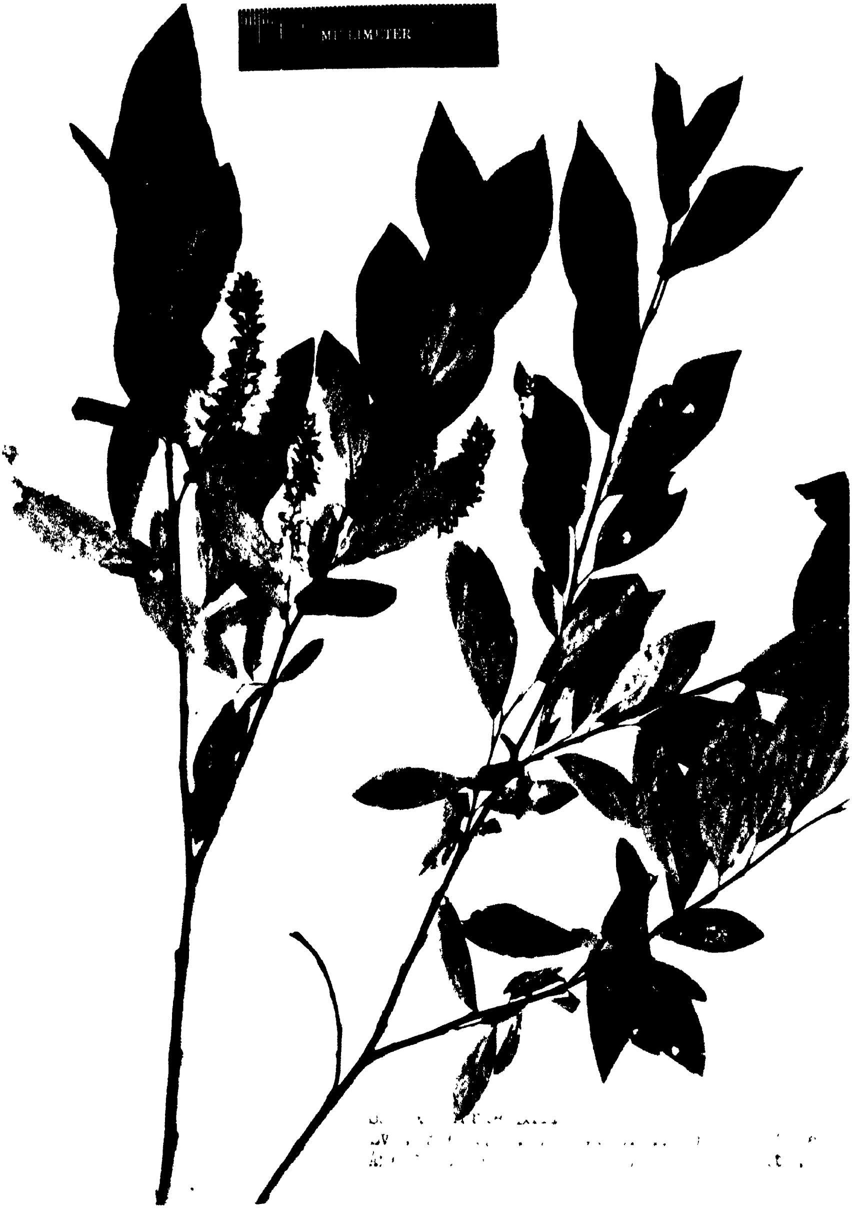
Salix Parksiana Ball. Staminate flowering branchlet with mostly juvenile leaves. × ¾



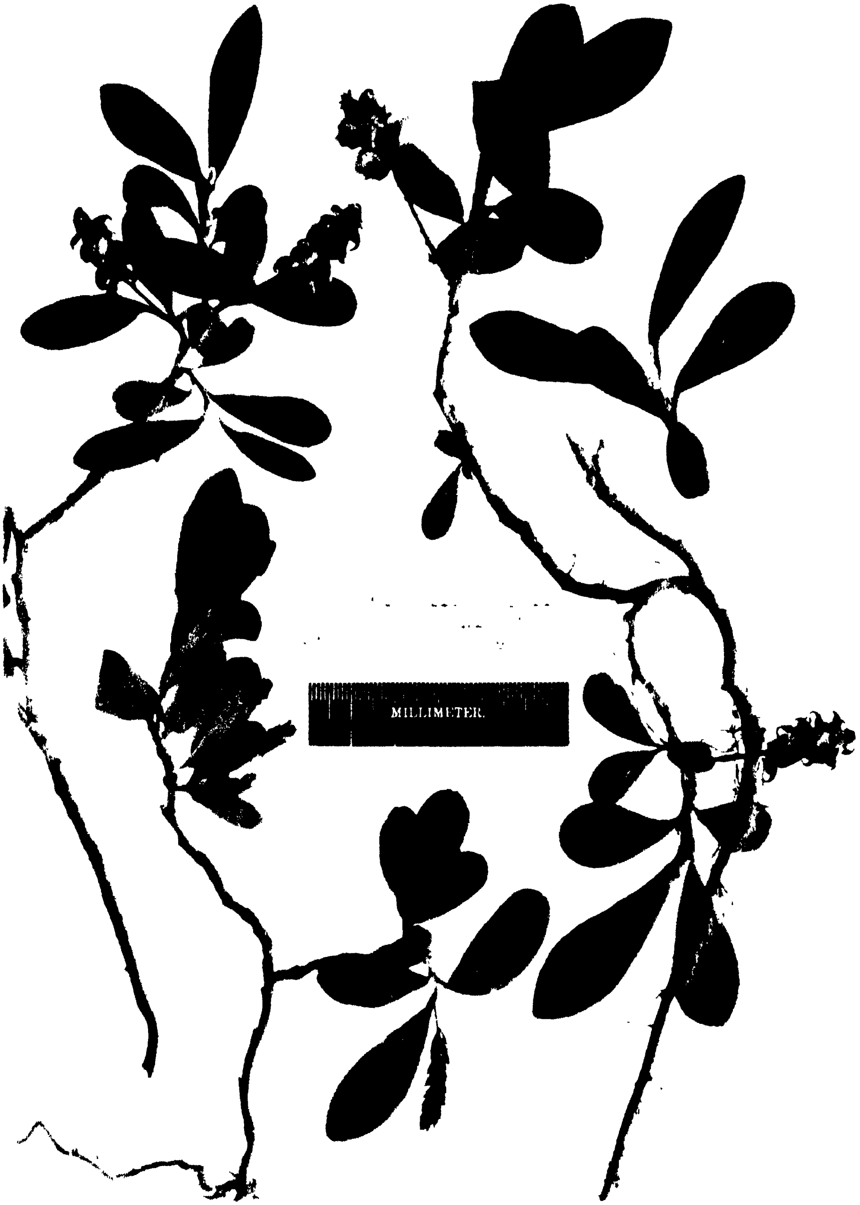
Salix Tracyi Ball. Fruiting branchlet showing full-grown leaves, indicating the characteristic late flowering. $\times \frac{3}{4}$



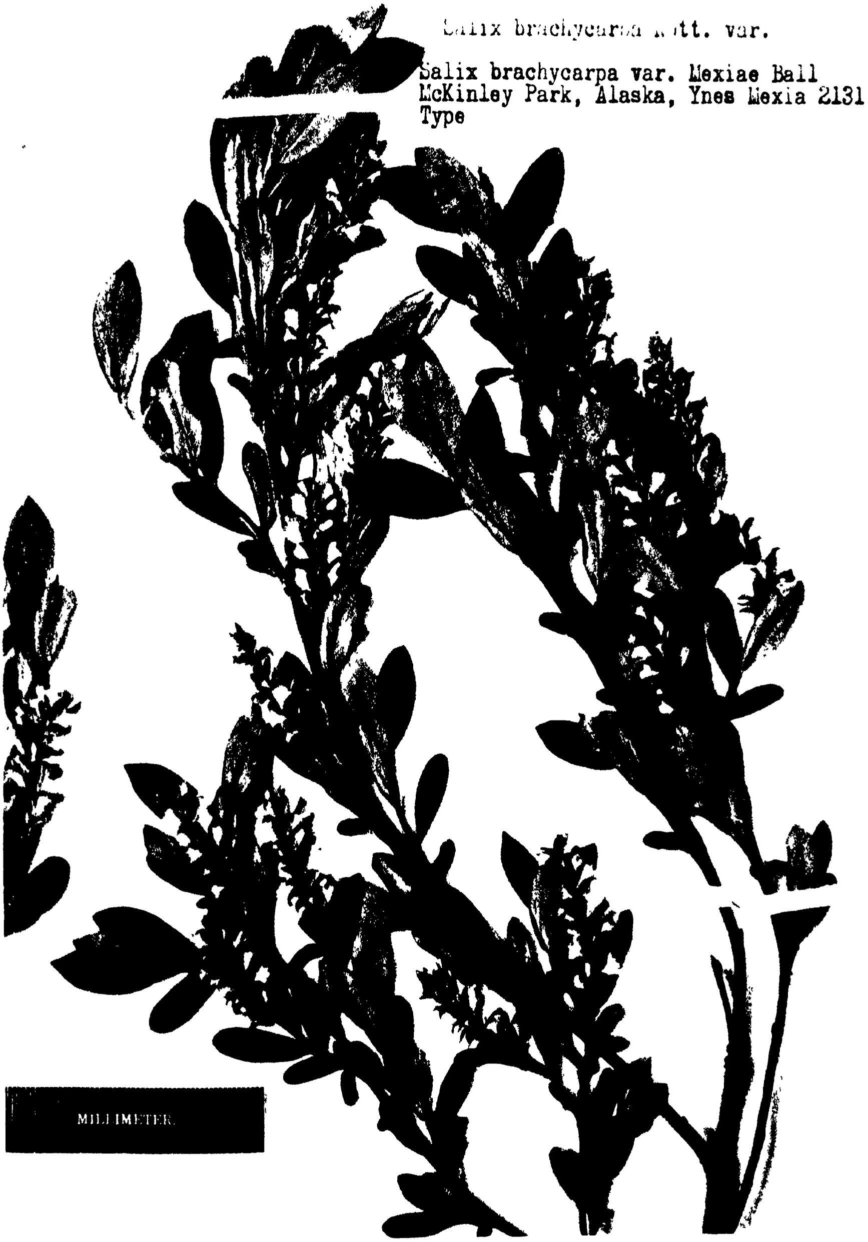
Salix Tracyi Ball. Branchlet from the staminate type collection (cotype from Herb. Ball). × ¾



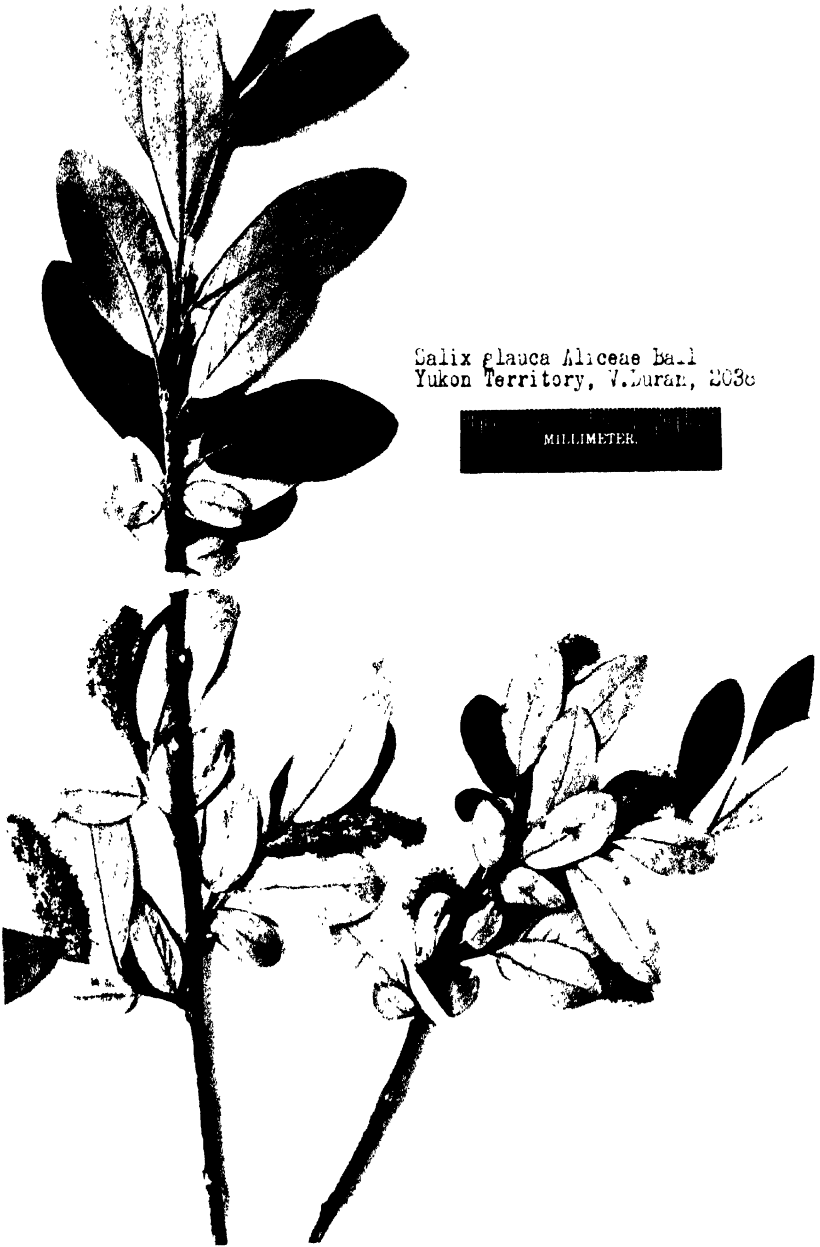
Salix Farrae Ball. Foliage branchlet (portion of pistillate type specimen) and fruiting branchlet. × ¾



Salix Setchelliana Ball. Portions of pistillate and staminate type specimens. × 3/4


Salix brachycarpa Nutt. var.
Salix brachycarpa var. Mexiae Ball
McKinley Park, Alaska, Ynes Mexia 2131
Type
MILLIMETER

Salix brachycarpa var. *Mexiae* Ball. A portion of the pistillate type specimen. × ¾



Salix glauca var. *Aliceae* Ball. Portion of a vigorous staminate branchlet showing the elliptic oval blades with rounded bases. × 3/4

THE NUMBER AND MORPHOLOGY OF CHROMOSOMES IN THE GENUS MELILOTUS

BY

ALFRED E. CLARKE

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THE NUMBER AND MORPHOLOGY OF CHROMOSOMES IN THE GENUS MELILOTUS

BY

ALFRED E. CLARKE*

CLASSIFICATION OF MELILOTUS SPECIES

THE CLASSIFICATION of the genus *Melilotus* is at present unsatisfactory. The first adequate treatment of the genus was given by Seringe in De Candolle's Prodromus, Volume II (1825). He arranged the genus in three sections on the basis of pod characters, as shown in the following classification:

Section I. *Coelorutis* Ser. Pods wrinkle-veined.
Section II. *Plagiorutis* Ser. Pods with somewhat curved wrinkles.
Section III. *Campylorutis* DC. Pods concentric wrinkle-folded.

Taubert (1894) classifies the species of *Melilotus* as follows:

Section I. *Lopholobus* Boiss. Pods spongy-papery, short, with 8–10 somewhat undulating longitudinal ribs.
Section II. *Campylorytis* DC. (*Gyrorytis* Koch). Pods concentric wrinkle-folded.
Section III. *Plagiorytis* Ser. Pods with light curved wrinkles.
Section IV. *Coelorytis* Ser. Pods wrinkle-veined.
  A. Plants biennial.
  B. Plants annual.

Schulz (1901) divides the genus into two subgenera and these are further divided into sections according to the following scheme:

Subgenus A: *Eumelilotus* O. E. Schulz.
  Biennial. Seeds smooth. Sutures splitting open ventrally.
  Section I. *Coelorytis* Ser.
Subgenus B: *Micromelilotus* O. E. Schulz.
  Annual. Seeds rough. Sutures not splitting open ventrally.
  Section II. *Laccocarpus* O. E. Schulz.
  Section III. *Plagiorytis* Ser.
  Section IV. *Campylorytis* Ser.
  Section V. *Lopholobus* Boiss.

A comparison of the classifications of Seringe (1825), Taubert (1894), Schulz (1901), and Hegi (1923) shows considerable conflict. Many of the species listed by Seringe are, according to Index Kewensis, only synonyms. Oddly enough, Seringe places *M. arvensis* Wallr. (= *M. officinalis*) in the subsection *Plagiorutis* while synonymous species are placed in the section *Coelorutis*. Taubert (1894) makes the same error. Examination of the pods shows that *M. officinalis* belongs in the subsection *Coelorutis*. Schulz places *M. tauricus* (M.B.) Ser. in one subsection and *M. neapolitanus* Ten. in another. According to Index Kewensis both are synonyms for *M. gracilis*. Each of the four keys lists *M. altissima* Thuill. as a distinct species, but Index Kewensis lists it as a synonym of *M. officinalis*. These and other discrepancies show clearly the need for a thorough study of the taxonomy of the genus. As a small contribution toward this end the present study of the number and morphology of the chromosomes of a number of species and strains of the genus *Melilotus* was undertaken.

---

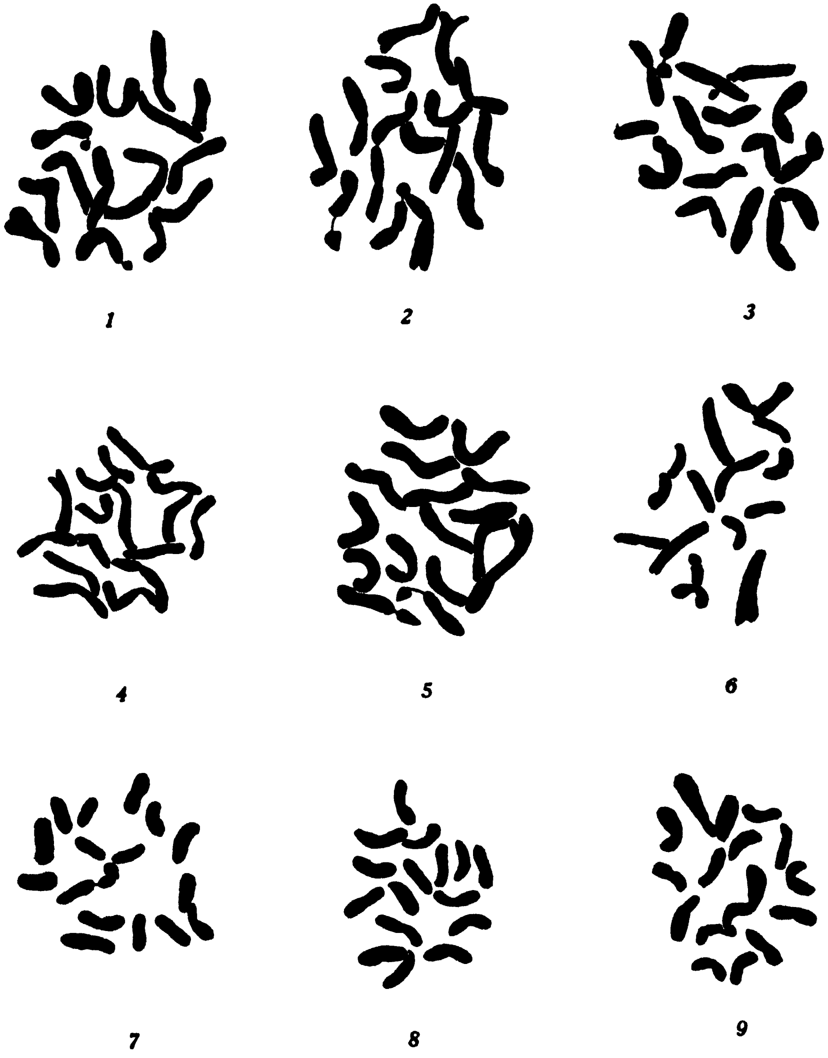
* National Research Fellow in the Biological Sciences.

Smith (1927) has classified species of *Melilotus* according to habit of growth and habitat. He notes that the biennial species of *Melilotus* are, as a rule, native to regions colder than the regions to which the annual species are indigenous. Smith suggests that some species which are biennial in colder regions may become annual in warmer regions. In support of this view he cites *M. alba* Desr. var. *annua* Coe, which is known to have arisen from *M. alba* Desr., in Alabama.

CYTOLOGICAL STUDIES IN THE TRIFOLIEAE

Castetter (1923) reports that in both *Melilotus alba* and *M. alba* var. *annua* the haploid number of chromosomes is eight. Elders (1926) reports the diploid number of chromosomes in *M. alba* and in *M. officinalis* as sixteen. Fryer (1930) finds sixteen chromosomes in the root tips of *M. sulcatus* Desf., *M. officinalis* (L.) Med., *M. alba* Med., and *M. indica* All. He notes that one pair of chromosomes in *M. alba* possesses satellites, while no satellites were observed in the other three species. In *M. indica* one pair of chromosomes appears to have two constrictions in each chromosome. In *M. sulcatus* the chromosomes are shorter than in the other three species.

Chromosome counts have also been obtained in certain other species of Trifolieae. Fryer (1930) reports sixteen chromosomes as the diploid number in *Trigonella coerulea*, *T. foenum-graecum*, and *T. cretica*. According to Tischler (1931) Tschechowa gives the haploid number of chromosomes in *T. polycerata* as fourteen. In *Medicago* species, Fryer (1930) reports a series of fourteen, sixteen, and thirty-two chromosomes in the diploid condition. In *Trifolium*, Wexelsen (1928) reports a simple polyploid series without intermediate numbers in which $n = 7$, 8, 14, 16, 24, about 48, and about 130. The basic numbers of this series are seven and eight. Tischler (1931) cites *T. pannonicum* as having ninety chromosomes according to Tschechowa. The same investigator finds 32 as the haploid number in *Ononis reclinata.* A study of the literature fails to show any counts for the genus *Parochetus,* which, according to Index Kewensis, consists of a single species. It will be noted that throughout the Trifolieae the basic chromosome numbers are 7 and 8, the latter being more frequent.



Figs. 1–9. Somatic chromosomes of *Melilotus* species.

All drawings were made with the aid of a camera lucida and a Leitz microscope equipped with a 2 mm. oil objective, apert. 1.32, and 15× oculars. Magnification of figures ×2700.

1. *Melilotus alba*
2. *Melilotus officinalis*
3. *Melilotus wolgica*
4. *Melilotus indica*
5. *Melilotus italica*
6. *Melilotus speciosus*
7. *Melilotus messanensis*
8. *Melilotus sulcata*
9. *Melilotus segetalis*

MATERIALS AND METHODS

Seeds used in this study were provided by the following: Dr. L. W. Kephart, of the United States Department of Agriculture; Dr. R. A. Brink, of the University of Wisconsin; Dr. L. E. Kirk, Dominion Agrostologist, Ottawa; Dr. M. Ufer, of the Kaiser Wilhelm-Institut für Zuchtungsforschung, Müncheberg i. Mark; the Royal Botanic Gardens, Kew; and the University of Algiers.

Somatic metaphases of root tips have been used exclusively for chromosome counts. Root tips were obtained from young plants, usually from about four to six inches high. Some material was fixed in Flemming (medium strength) but the greater number of the investigations and all the drawings were made on material fixed for from twelve to twenty-four hours in Karpechenko's solutions (Hollingshead and Babcock, 1930).

Root tips were sectioned at 10–14μ and stained with Heidenhain's iron haematoxylin, or iodine-gentian violet.

CYTOLOGICAL OBSERVATIONS

Since no chromosome counts for the genus *Parochetus* have been recorded, it seemed desirable to examine the root tips of *Parochetus communis* Buch.-Ham. As previously mentioned, according to Index Kewensis this is the only species belonging to the genus. *P. communis* (fig. 10) has sixteen chromosomes. It agrees, therefore, in chromosome number with the other genera of the Trifolieae.

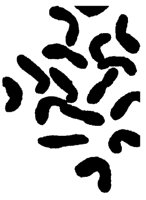


Fig. 10. Somatic chromosomes of *Parochetus communis.*

In the following species of *Melilotus* the somatic chromosome number is 16: *Melilotus alba* Desr., *M. alba* Desr. var. *annua* Coe, *M. officinalis* (L.) Desr., *M. wolgica* Poir., *M. indica* All., *M. italica* (L.) Lam., *M. speciosus* Dur., *M. messanensis* All., *M. sulcata* Desf., and *M. segetalis* Ser.

In *Melilotus alba* (fig. 1) one pair of chromosomes is characterized by the occurrence of large satellites. The chromosome varies from V-shape to U-shape. *M. alba annua* has a chromosome complex similar to that of the biennial type, and so far as could be determined is indistinguishable from it. This result is not surprising, since Smith (1927) has reported that the annual habit is inherited as a simple dominant.

In *Melilotus officinalis* (fig. 2) a pair of conspicuous satellites are to be observed, but the satellited chromosomes differ from those of *M. alba* in being shorter. In this species the satellited chromosomes are the shortest.

Under the name of *Melilotus suaveolens,* certain lots of yellow-flowered sweet clover have also been obtained from Dr. L. E. Kirk and Dr. L. W. Kephart. Concerning this material Dr. Kephart has written, "We have imported more than a dozen numbers of sweet clover under the name of *Melilotus suaveolens;* some of them produced plants quite different in their habit of growth from *M. officinalis,* yet not sufficiently distinct morphologically to make them agree with the description of *M. suaveolens.*" A cytological examination fails to reveal any differences between these lots of so-called *M. suaveolens* and strains of recognized *M. officinalis.* F_2 progenies from crosses between so-called *M. suaveolens* and *M. officinalis* have been grown in the field. The F_2 plants varied in appearance from one parent type to the other, showing all possible intergradations and making classification extremely difficult. Since these sorts readily cross to give fully fertile hybrids, and since no differences in chromosome morphology have been found, it appears probable that the sorts examined are only varietal strains of *M. officinalis.*

Melilotus wolgica (fig. 3), like *M. alba* and *M. officinalis,* has a pair of satellited chromosomes. The chromosome complex appears to resemble that of *M. alba* very closely. Both species belong to the same section, *Coelorytis.* While the two species are readily distinguishable from each other morphologically, particularly because of the longer pedicels of *M. wolgica,* it may well be that they are closely related. Hybridization studies, which are now being carried out, should throw further light on this question.

In *Melilotus indica* (fig. 4) the chromosomes are very slightly smaller than in *M. alba, M. officinalis,* and *M. wolgica.* One pair of chromosomes appears to have two constrictions; the remaining ones have a single median constriction. On the basis of size, the shortest pair of chromosomes may be distinguished from the others. No satellites were observed.

Melilotus italica (fig. 5) possesses the largest chromosomes of any species examined. One pair of large satellites or chromosome fragments is present. Frequently they do not appear to be attached to or connected with any other chromosomes; in this respect these satellites seem to behave like those noted in certain *Trifolium* species by Wexelsen (1928).

Melilotus speciosus (fig. 6) possesses chromosomes of two different sizes. Three pairs of chromosomes are long, like those in the species just described, while the remaining five pairs are distinctly shorter. No satellites were observed.

Melilotus messanensis (fig. 7) has much shorter chromosomes than those of any of the species so far considered, every pair being about the same length as the short chromosomes of *M. speciosus.* Each chromosome appears to have a median constriction. A pair of conspicuous satellites or chromosome fragments is present. As in *M. italica,* they frequently appear to lie free on the metaphase plate.

The chromosomes of *Melilotus sulcata* (fig. 8) are extremely short, resembling those of *M. messanensis.* No satellites were observed.

In *Melilotus segetalis* (fig. 9) seven of the eight pairs are short, as in *M. sulcata.* The remaining pair, however, is distinctly larger than the others. No satellites were observed. According to Index Kewensis (1895), *M. segetalis* is probably synonymous with *M. sulcata.* Since they can be distinguished cytologically, it appears probable that they deserve to be considered as distinct species. A study of species hybridization should yield additional evidence on this question.

DISCUSSION

In a study of eleven of the forty-four species of *Melilotus* recognized by Index Kewensis all were found to possess eight pairs of chromosomes. No polyploid series such as one finds in *Trifolium* and *Medicago,* was observed. All sections of the genus are represented in this study except *Lopholobus,* which consists of a single species, *M. bicolor,* of which it was not possible to obtain seed.

In *Melilotus* the cytological observations have tended on the whole to support Seringe's classification based on morphological characters. The small chromosomes of the species belonging to the section *Campylorytis* (*M. messanensis, M. sulcata,* and *M. segetalis*) serve to differentiate them from the other groups. As pointed out earlier, *M. speciosus,* representing the section *Plagiorytis,* appears to occupy an intermediate position with its chromosomes falling into two well marked size groups.

Schulz (1901) has broken up the *Coelorytis* section, as presented by earlier authors, and has placed the annual species in a new section, *Laccocarpus.* It would seem preferable to follow the earlier usage. It is true that *M. alba, M. officinalis,* and *M. wolgica* resemble one another very closely in chromosomal morphology. However, *M. italica* and *M. indica,* grouped together in the section *Laccocarpus,* have rather widely different chromosome complexes. A more serious difficulty is found in attempting to classify *M. alba annua,* a subspecies not mentioned by Schulz. On both morphological and cytological grounds it is obviously closely related to *M. alba,* and placing it in a different section of the genus would be unsatisfactory.

Unfortunately these cytological studies have not proved very helpful in providing additional information on the taxonomy of the genus, but some species belonging to the same section of the genus have been distinguished from one another on the basis of chromosome size, presence or absence of satellites, and number of constrictions. A cytological examination is apparently of value in respect to some plants in determining whether or not a particular strain belongs to a certain species.

An interesting attempt has been made by Sveshnikova (1927) to classify *Vicia* species on the basis of chromosomal morphology. She finds that a key based on chromosomal morphology corresponds closely to Ascherson's key based on external morphology. But Wexelsen (1928), working with *Trifolium,* fails to discover any close relationship between the chromosome complex and the taxonomic position and morphological characters of the various species. He suggests that hybridization has not played a dominant rôle in the differentiation of this genus, and that variability in chromosomal morphology results chiefly from mutational changes in species isolated by interspecific sterility. He further suggests that the evolution of the chromosome complexes in *Trifolium* is the result of parallel variation. For example, the presence of a pair of satellited chromosomes in very different sections of the genus may be the consequence of independent parallel variations and need not indicate that they have been derived from a common source. Fryer (1930) reports that in *Medicago* there is a general agreement between his cytological findings and the taxonomic classification by Taubert.

The observations made on the satellited chromosomes in the present study are comparable to those made by Wexelsen in *Trifolium.* It may well be that some parallel variation has taken place in the evolution of the chromosome complexes of the different sections. It is hoped that additional data on the relationships of the various species will be obtained from a study of species hybrids.

ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Professor E. B. Babcock for his kindly interest and helpful criticism. He is indebted also to the many workers who have furnished seeds.

SUMMARY

1. Literature dealing with the taxonomy of the genus *Melilotus* is reviewed. A comparison of several botanical keys shows that many discrepancies exist and that a thorough revision of the classification of the genus is required.

2. The diploid number of chromosomes in *Parochetus communis* is sixteen.

3. The diploid number of chromosomes is sixteen in the following species: *M. alba, M. alba annua, M. officinalis, M. wolgica, M. indica, M. italica, M. speciosus, M. messanensis, M. sulcata,* and *M. segetalis.*

4. Chromosomes have been found to differ in size, presence or absence of satellites, and number of constrictions. Certain species can be distinguished from one another on the basis of differences in chromosomal morphology.

5. Certain strains of yellow-flowered biennial sweet clover, obtained under the name *M. suaveolens,* are probably varietal forms *M. officinalis.*

6. Species belonging to the section *Campylorytis* are cytologically distinct from the other species studied because of the smaller size of their chromosomes. Section *Plagiorytis* appears to occupy an intermediate position, with the chromosomes falling into two well marked groups when classified on the basis of size.

7. In general, the cytological studies confirm the accepted taxonomic groupings made by Seringe.

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